The Effects of Logging on Amphibian Life History

by

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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy,
School of Zoology, University of Tasmania
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Declaration: I declare that this thesis contains no material which has been previously accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and, to the best of my knowledge and belief, no material previously published or written by another person, except where due acknowledgement is made in the text of the thesis.

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Abstract

I assessed the value of life history studies as an approach to evaluating the impact of recent clearfell logging on pond breeding frogs. I conducted a number of distinct studies investigating different aspects of amphibian life history in response to logging using *Crinia signifera* and *Litoria ewingii* as my model species.

Life history studies were successfully able to:

- assess breeding site suitability for *L. ewingii* by correlating habitat components with life history traits and fitness. Breeding ponds that maximised the fitness of *L. ewingii* were higher elevation ponds with reduced shading, steeper bank slopes and reduced pond isolation. The outcomes of the study enabled me to provide management guidelines for the construction of ponds designed to maximise the fitness of target species.
- determine the consequences of decreased shading associated with vegetation removal around permanent and ephemeral ponds for larval fitness in *L. ewingii.* Increased shading around permanent ponds resulted in reduced survival. Increased shading in ephemeral ponds resulted in decreased developmental rate and a higher variation in size at metamorphosis. The outcome of the study provided guidelines for vegetation management around breeding sites.
- investigate landscape use of the commercially managed forest by *Crinia signifera* in order to determine the fraction of the forest used as habitat, the effect of logging upon movement through the forest, and the consequences for reproductive output. *Crinia signifera* was distributed widely throughout the forest landscape for up to

500 m around each permanent breeding site. Ponds surrounded by unlogged forest were colonized almost two times faster than ponds surrounded by logged forest. As a result, total reproductive output at unlogged ponds was double that of ponds surrounded by recently logged coupes.

- demonstrate that logging can affect maternal reproductive investment and offspring fitness in both *Crinia signifera* and *Litoria ewingii*. Eggs were collected from ponds located in either logged or unlogged forest and raised to metamorphosis under common laboratory conditions. Egg size was greater at unlogged than logged sites for both species. For *L. ewingii*, size at hatching was also greater at unlogged sites; but for *C. signifera* size at hatching was independent of logging treatment. For *L. ewingii*, survival to metamorphosis was greater at logged sites. For *C. signifera* survival at metamorphosis did not differ with logging treatment despite greater survival at hatching in eggs from logged sites.
- confirm that fluctuating asymmetry has limitations as an indicator of ecosystem stress and the population health of *C. signifera* in response to logging. The findings indicate a decrease in fluctuating asymmetry (and implied environmental stress) but also a decrease in body size and body condition (i.e. fitness) as a result of logging. There was no significant relationship between the levels of subtle asymmetry in individuals and the following life history traits: clutch size, clutch dry mass, average egg dry mass, oviduct dry mass, testes size, age, body size and body condition.

My research confirms that logging significantly influences the life history of *L. ewingii* and *C. signifera*. I argue that, by linking changes in life history traits with assessments of

fitness, life history studies can be used to understand *why* species respond to logging in the ways they do. In this way, life history studies can provide data on which to base constructive, defensible recommendations for the ecologically sustainable management of commercial forests with regard to the frog species that use them. Life history studies are a valid experimental approach that can be used to redress the data deficit relating to the impact of logging on amphibians in Australia.

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As with everything in life, this project could not have been completed without the help and support of many others. As a result, this thesis is as much theirs as it is mine. In particular, I would like to acknowledge the help and support of the following:

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Table of Contents

Chapter 1: Introduction

Previous studies using amphibians as bio-indicators of logging have measured species richness or abundance of species. Given the high diurnal and annual variability of amphibian activity, these techniques require significant effort and resources. As a consequence, research investigating the impact of forest harvesting on amphibians in Australia is limited. The lack of forestry related studies requires redressing if forest management plans are to be effective in providing appropriate management prescriptions for all vertebrate fauna. This project aims to assess the value of amphibians as bio-indicators of logging practices by examining life history and population health rather than the measurement of species richness or abundance. The project

- addresses issues of conservation and sustainable forest use and seeks to ensure a better understanding of ecological processes within forests;
- addresses an area of sustainable resource management in Australia with large knowledge gaps;
- is applicable on a national scale since the predominant species of interest in the study (*Litoria ewingii* and *Crinia signifera*) have ranges within a significant area of Australia's commercial forests, and;
- has value to a wide range of industry stakeholders, since managed forests involve both private and public ownership, and forest management invokes considerable public debate.

GENERAL RESEARCH AIMS

It was the aim of the project to

- study the biology of *L. ewingii* and *C. signifera* in the southern commercial forests of Tasmania and hence improve knowledge of ecosystem process and function with respect to amphibians;
- determine the consequences of environmental change resulting from logging for amphibian life history;
- assess the value of amphibian life history as a bio-indicator of land management practices in order to facilitate optimal decision making by land managers.

PRESENTATION OF THE THESIS

This thesis is presented as a compilation of papers that have been submitted for publication. I am the primary author on all submitted manuscripts having undertaken the data collection, data analysis, and preparation; however, I have also recognized the contributions of others by acknowledging them as co-authors where applicable. Publication status and authorship of individual manuscripts varies and details are provided at the beginning of each chapter.

By necessity, there is some repetition of bibliographic, study area and study species descriptions between data chapters. These descriptions are brief and a comprehensive overview of the study area and the study species is provided in Chapter 2. Formatting between chapters is not necessarily uniform because of the requirements of different journals. The content of each manuscript remains as submitted.

OUTLINE OF THE THESIS

Chapter 1: Introduction and overview of the thesis.

Chapter 2: Describes the study area and the two study species.

Chapter 3: Reviews the potential of life history studies as a novel approach for investigating the impact of logging on pond breeding anurans.

Chapter 4: Determines breeding site characteristics that optimize the fitness of *Litoria ewingii* in order to provide management recommendations for the anthropogenc construction of appropriate breeding sites.

Chapter 5: Assesses how differences in pond shading affect the larval life history of *Litoria ewingii* and provides recommendations for vegetation management around pond margins.

Chapter 6: Investigates the impact of logging and pond isolation on pond colonization in order to examine landscape use and the effect of logging on the mobility of amphibians.

Chapter 7: Examines if logging alters maternal reproductive investment and offspring fitness.

Chapter 8: Assesses Fluctuating Asymmetry as a Means of Monitoring Population Health in Response to Logging.

Chapter 9: Provides a synthesis of previous data chapters.

Appendix 1: Validates the use of aquatic funnel traps used in Chapter 4.

Appendix 2: Provides background life history characteristics for *Crinia signifera* in southern Tasmania.

Appendix 3: Examines the seasonal activity patterns of *Crinia signifera*.

PERMITS

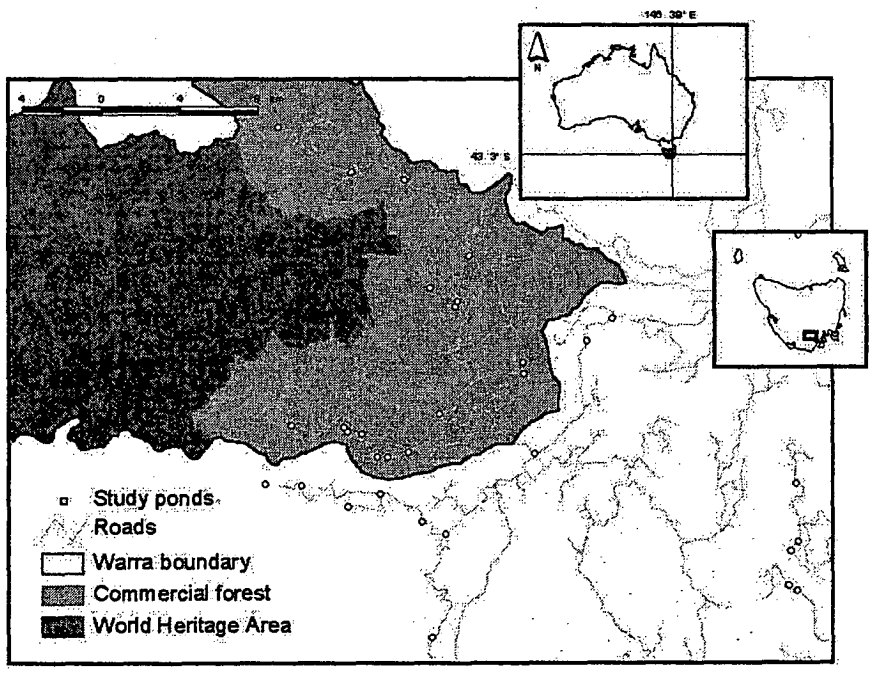
Research was conducted under Ethics Permit A0006021 issued by the University of Tasmania Animal Ethics Committee.

Chapter 2: Study Area and Study Species

THE WARRA LTER SITE

The study area was centred on the Warra Long Term Ecological Research (LTER) site in southern Tasmania. Where necessary, research was also extended beyond the boundaries of this site to incorporate bordering native forest areas and more distant native plantation areas (see Figure 1). Unless specifically mentioned, site descriptions presented below refer specifically to the Warra LTER, with the assumption that neighbouring forests do not differ significantly.

Figure 1. The study area



The Warra LTER is located within the Southern Forests of Tasmania, approximately 60 km south of Hobart (146° 40' east and 43° 04' south) and has an elevation range of 37-1260 m (Brown *et al.* 2001).

The Warra LTER was established in 1995 and has a total area of 15900 ha. The western portion of the site is World Heritage Area and the eastern part commercially managed forest (Packham 1995). The site is cooperatively managed by Forestry Tasmania, Tasmanian Parks and Wildlife Service, Forests and Forest Industry Council, Bureau of Rural Sciences, University of Tasmania, CSIRO and Cooperative Research Centre for Sustainable Production Forestry (Brown *et al.* 2001).

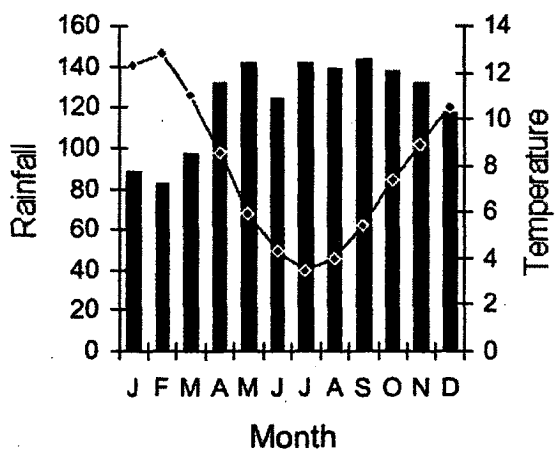
The Warra LTER site is part of a network of such sites across the world. As the name implies, the aim of LTERs is to encourage long term, inter-disciplinary research in order to better understand ecological processes occurring within particular ecosystems and to identify and provide solutions to ecological problems.

The specific aims of the Warra LTER centre on developing an understanding of ecological processes in Tasmania's wet *Eucalyptus obliqua* forests and the demonstration and development of sustainable forest management practices (Warra LTER pamphlet).

Climate

The average annual temperature and rainfall at the site is 7.9 °C and 1477 mm, respectively (www.warra.com). Precipitation falls throughout the year (Packham 1995) but average monthly rainfall and number of storms show a strong winter bias (Ringrose *et al.* 2001) (see Figure 2). Mean temperatures are lowest during July and highest during February.

Figure 2. Average monthly rainfall (mm; columns) and temperature (°C; line) from the Manuka Road weather station

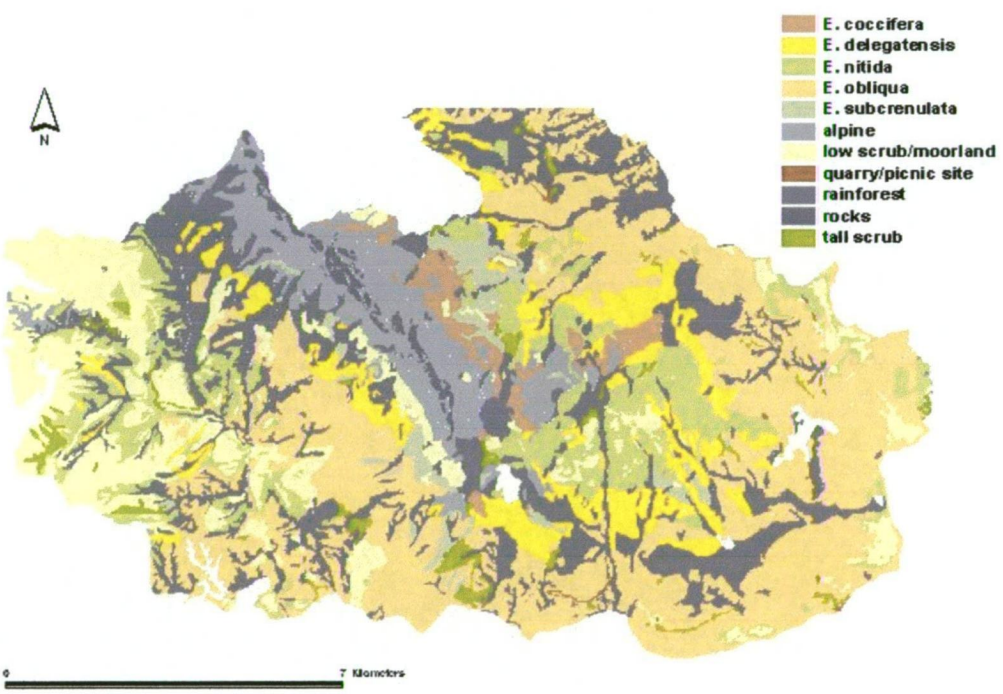


Spatial modelling of weather patterns using ANUCLIM (http://cres.anu.edu.au/outputs/anuclim.html) shows a marked climatic gradient across the site due predominantly to the westerly weather system and the altitudinal range (Corbett and Balmer 2001). Higher rainfall and lower temperatures occur at higher elevations and in the west.

Forest Types

Eucalyptus obliqua is the most widespread forest type at the site (Neyland *et al.* 2000) and is also the most widespread commercially harvested forest type in Tasmania (Corbett and Balmer 2001). The site also contains moorland, alpine vegetation, temperate rainforest, riparian forests, conifer forest and scrub (Brown *et al.* 2001). For the distribution of different vegetation types at Warra, see Figure 3.

Figure 3. Forest types at the Warra site (source: Forestry Tasmania)



Forest Management Practices

Both logging and fire have influenced the stand age characteristics at the Warra site and, as a result, a full range of successional forest stages is present (www.warra.com).

Standard logging practices in wet schlerophyll and mixed forests consist of clearfell, burn and aerial sowing with eucalypt seed (CBS) on a rotation of 90 years (Hickey and Neyland 2000). Clearfelling aims to mimic the natural disturbance regimes of catastrophic fires that are common in this area and for this forest type. Such fire and silvicultural regimes both result in the subsequent growth of even aged stands. Post-logging burns release available nutrients so as to prepare the seedbed for rapid regeneration of eucalypt seedlings.

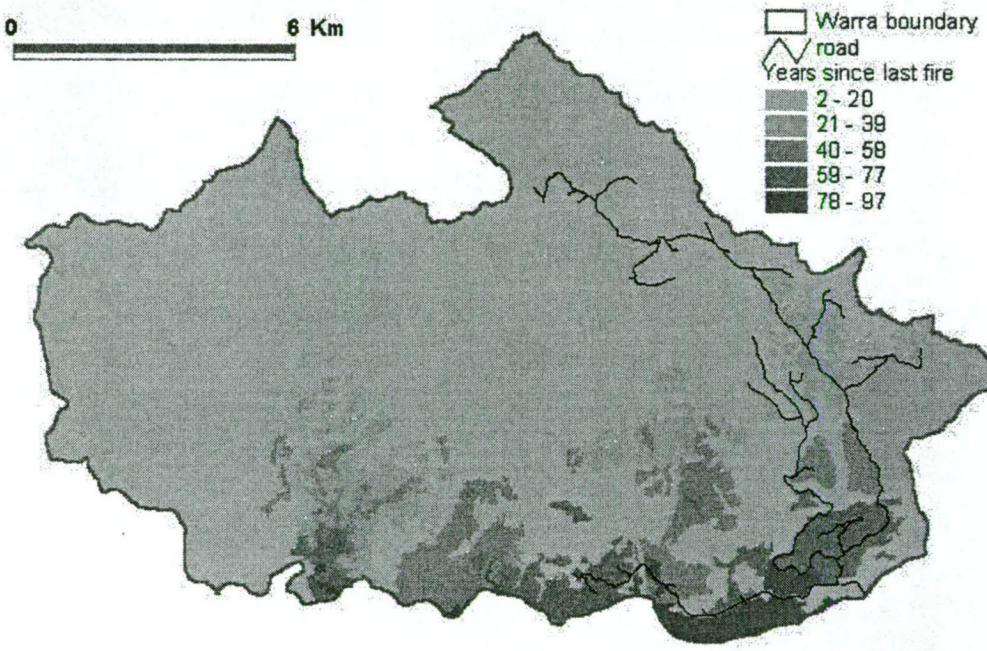
Due to concerns regarding aesthetics, a reduction in late successional species and/or structures, and a decline in the special species timbers (Hickey *et al.* 2001), trials have also been set up at Warra to investigate alternative silvicultural techniques. The following five alternative practices are being investigated: CBS with understorey islands, stripfell/patchfell, 10% dispersed retention, 30% aggregated retention, and single tree/small group selection (Hickey *et al.* 2001). Where possible logged sites using the standard CBS techniques were used within the current study; however, some logged sites from the alternative silvicultural trials were utilized when insufficient standard CBS sites were available.

Fire History

Hickey *et al.* (1998) found that just over half the tall eucalypt forests at Warra occur as mature and oldgrowth stands and that these had been established following fires between the early 1500s and 1850. Seventeen percent of the forest has been subjected to fire in the last century and these fires have been sufficiently intense to result in pure regrowth

stands. Twenty-six percent of the forest has also been burnt by at least one fire in the past century resulting in mixed stands of regrowth and mature trees. The length of the natural fire rotation was calculated to be 448 years (Hickey *et al.* 1998). Figure 4 shows the fire history of the Warra site.

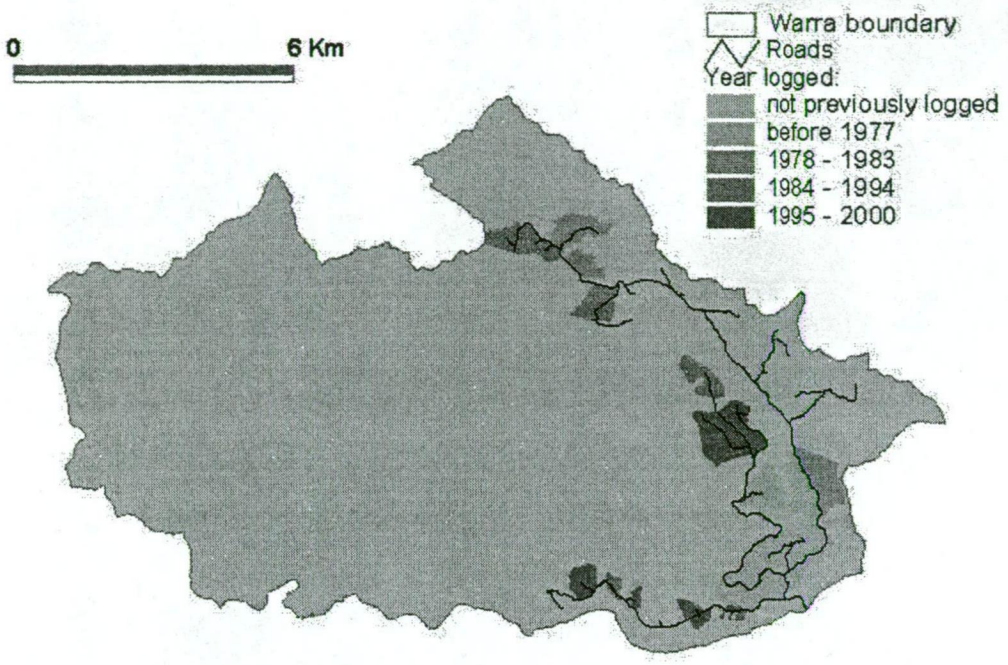
Figure 4. Fire history of the Warra site (source: Forestry Tasmania)



Logging History

Logging in the area dates back to the early 1800s when Huon pine harvesting began in the Huon River area. Access to the Warra site was possible only after 1969 when a bridge was constructed across the Huon River (Packham 1995). Figure 5 shows the recent logging history at Warra.

Figure 5. Logging history of the Warra site (source: Forestry Tasmania)



Fire Management Ponds

Forestry Tasmania has constructed numerous small-medium sized, permanent ponds along roadsides throughout the commercial forests to provide sources of water for the management of fire. The increased prevalence of such standing water as a result of forest management activities has resulted in a greater number of amphibian breeding sites within the forest than would otherwise be available. The study species used within this thesis aggregate around fire management ponds during the breeding period, thus providing convenient locations at which to study them.

STUDY SPECIES

Tasmanian Frogs

Eleven frog species occur in Tasmania. Eight belong to the family Myobatrachidae *(Crinia signifera, C. tasmaniensis, Geocrinia laevis, Pseudophryne semimarmorata, Bryobatrachus nimbus, Limnodynastes dumerilii, L. tasmaniensis, L. peronii*) and 3 to the family Hylidae (*Litoria ewingii, L. burrowsae* and *L. raniformis*). Of these *C. tasmaniensis, L. burrowsae* and *B. nimbus* are endemic to the State. The breeding seasons of Tasmanian anurans fall broadly into three categories: (a) year-round breeders (*Crinia signifera, Litoria ewingi*), (b) late summer breeders *(G. laevis, P. semimarmomarta*) and (c) spring and summer (the remaining species) (Littlejohn and Martin 1974). Although *C. tasmaniensis* and *L. burrowsae* are also known to occur at the WARRA site, *L. ewingii* and *C. signifera* were the only amphibian species located in sympatry within the more limited study areas used in this research.

Of the species found in Tasmania, *L. ewingii* and *C. signifera* were chosen as study species within the present study because:

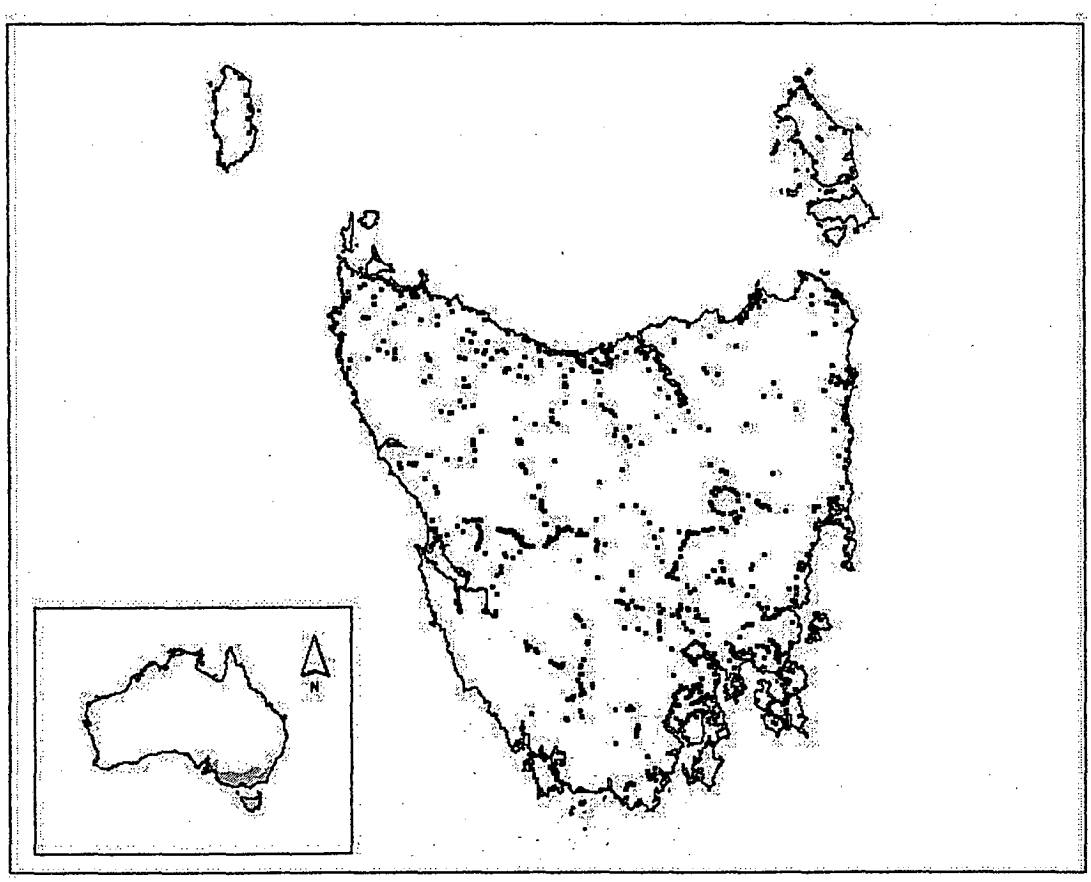
1. these species have widespread distributions, both within Tasmania and throughout south-eastern Australia. This ensures that the findings of the present study have a wider national context.
2. both species are abundant, ensuring that small sample size did not compromise statistical power and hence the findings of the research;
3. both species have very flexible life histories; and

4. they have different life histories. For example, *L. ewingii* has a longer larval developmental period, has a predominantly pelagic larval behaviour, and has larger clutch, egg, larval and adult body size as opposed to *C. signifera*. These differences may predispose one species to a particular research method and *vice versa*.

Litoria ewingii

Litoria ewingii is widely distributed throughout south-eastern Australia and is found throughout Tasmania (Figure 6). The species has also been introduced to New Zealand (Cree 1984).

Figure 6. Distribution of *L. ewingii* in Tasmania based on Gspot database NPWS (Australian range based on Cogger (2000))



L. ewingii is found in a wide range of habitats and, despite being classed as a tree frog, is primarily terrestrial in nature. It is commonly found under logs and debris on the ground when not at the breeding site (Littlejohn and Martin 1974).

The following description of the adult frog is sourced from Robinson (1996) (refer to Figure 7 left, for photograph). Pale to cream-brown on the back, with a broad band running down the back with scattered darker flecks. A dark brown or black stripe runs from the snout through the eye and tympanum to the shoulder, becoming indistinct on the flanks. There is a pale stripe below this dark stripe, running from the eye to the base of the upper arm. The belly is yellowish-white, cream or white. The backs of the thighs and the groin are yellow to red-orange. There is no spotting or marbling in the groin or the thighs. The skin is smooth or with low tubercles, and the belly is granular. The toes are half webbed and there are small toe discs, only slightly wider than the toes. There are vomerine teeth between the choanae and maxillary teeth. *Litoria ewingii* has a snout vent length of up to 45mm. Males can be distinguished from females during breeding by a grey colour under the chin and brown nuptual pads on the inner fingers (Martin and Littlejohn 1982).

Figure 7. *L. ewingii* adult (left), tadpole (middle), and eggs (right)

Litoria ewingii breeds in both permanent and ephemeral waters (Sokol 1984). On the mainland the species breeds in both standing and flowing water, but in Tasmania breeding is limited to lentic systems. In Tasmania breeding occurs predominantly during early spring to early summer; however, limited breeding during autumn may also occur. The species has an extended breeding period and can be heard calling year round from the ground, low vegetation and while floating amongst vegetation (Robinson 1996). Calling consists of a whistling series of "weep eep eep eep" notes (Robinson 1996).

Litoria ewingii lays eggs in non-foamy jelly masses attached to submerged vegetation (see Figure 7 right). Clutch size ranges from 100-450 eggs with each clutch usually laid in separate, multiple clumps the size of which is dependent mainly on the vegetation (pers. obs). The eggs are pigmented and small with the egg capsule measuring approximately 5.0 mm in diameter (Martin and Littlejohn 1982).

Upon hatching embryos are black and have filamentous external gills. Larvae typically use the entire water column (Peterson *et al.* 1992) and larval morphology is consistent with this habitat preference. Older larvae have an hourglass shape, a large muscular tail and are relatively transparent in colour (presumably so that they are more difficult to see when suspended in the water column (Wheeler 1987) although the colour can vary from yellow to black in some conditions (see Figure 7 middle). They have a pale nasal stripe and a metallic, reflective ventral surface (Bridgeland 1998). The eyes are set laterally in the head, allowing good peripheral vision to enable predator avoidance and search for food (Millen 1995). A small area of the tail fin protrudes above and below the line of the

body (a characteristic of suspension feeders that spend time in the water column rather than on the substrate). There is a dextral anus and 2/3 mouth formula (Martin and Littlejohn 1982). In experimental conditions, both substrate use and predation from odonates was shown to increase at night (Peterson *et al.* 1992).

The larval period has been documented to range from 6-7 months (Martin and Littlejohn 1982), 4-5 months (Littlejohn and Martin 1974) and 1.5-2 months (Sokol 1984). Metamorphosis occurs predominantly in summer; however metamorphs have been seen in autumn and early spring (pers. obs.). At metamorphosis froglets have an average SVL of 14.24 ± 2.4 mm (pers. obs.).

Crinia signifera

Crinia signifera is widely distributed throughout Tasmania and south-eastern mainland Australia (Figure 8). The species is found in a wide range of habitats (Robinson 1996). The frog has an adult SVL range of 20-30 mm and the colour of the dorsal surface ranges from light grey through brown to almost black (Robinson 1996) (see Figure 9 left). There are 4-5 colour morphs (Clyne 1969) and both colour and morph can be highly variable within clutches, among clutches within populations and among populations. The ventral surface is granular with irregular black blotches on a white background (Martin and Littlejohn 1982) and the throat and chest of breeding males are dark grey (Robinson 1996). The fingers and toes are unwebbed but the toes are fringed and the palm has tubercles (Robinson 1996). There are no vomerine teeth (Robinson 1996) and the tympanic membrane is barely visible (Clyne 1969).

Figure 8. Distribution of *C. signifera* in Tasmania based on Gspot database, NPWS (Australian range based on Cogger (2000))

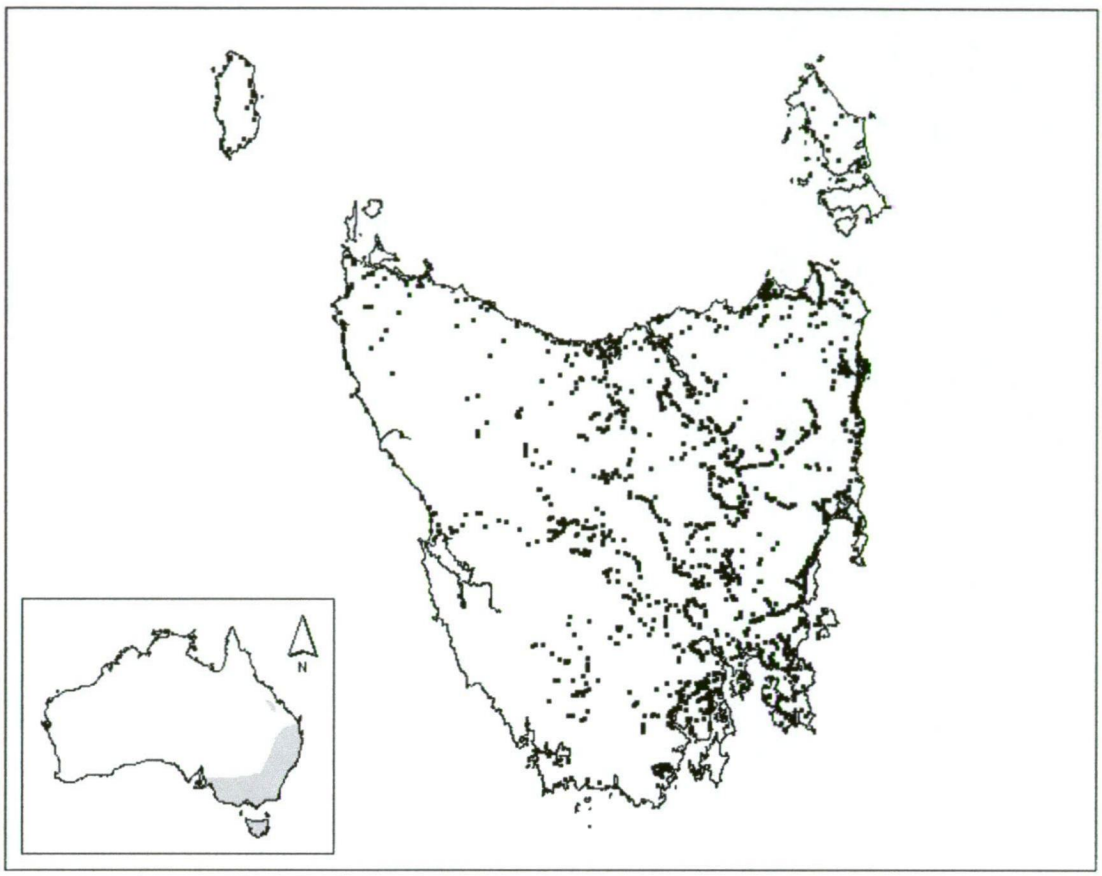


Figure 9. *C. signifera* adult (left), larvae (middle) and eggs (right)

The species breeds in both permanent and ephemeral sites and, in Tasmania, breeding is limited to lentic systems. The species calls throughout the year from the water's edge or whilst floating among vegetation and the call sounds like a 'crick crick crick' (Robinson 1996).

Breeding season varies with geographical location (Lemckert 2001). On the mainland of Australia the species breeds from mid-winter to early summer, with no reproduction occurring from mid-summer to late-autumn (Humphries 1979; Mac Nally 1985). Lemckert (2001), for example, found year round calling and breeding at his field site south of Sydney. Breeding in the Southern Forests of Tasmania occurs predominantly in early spring to mid-summer and any autumn breeding seems dependent on rainfall (pers. obs.).

Eggs are laid singly, attached to vegetation and other substrate at the bottom of the pond (see Figure 9 right). Egg size ranges from 1.3-1.6 mm (Tyler 1994). Williamson and Bull (1995) found clutch sizes of 68-273 eggs for a population in South Australia. However, clutch sizes of up to 500 eggs have been noted within the current study (pers. obs.).

Newly hatched tadpoles lack external gills and are about 5 mm in length (Martin and Littlejohn 1982). Older larvae are torpedo shaped (i.e. pointed at the anterior end) (see Figure 9 middle). They are not uniformly coloured but orange to tan to dark brown with randomly patterned spots of different colours. Most exhibit a 'v' shaped line of spots extending posteriorly from eyes (Wheeler 1987).

Larvae spend most of their time on the substrate of the water body (Peterson *et al.* 1992). Consequently, their eyes and nostrils are located dorsally to enable them to sense the surroundings. Similarly, mouthparts are located on the underside of the body to enable feeding on the substrate (Wheeler 1987). The anus protrudes through the ventral tail fin at 45° and the ventral tail fin does not protrude further than the depth of the body so as not to drag on the substrate (Wheeler 1987). The larvae spend large amounts of time inactive on the substrate, presumably to avoid predation, and move in short, sharp bursts (Peterson *et al.* 1992). Larval period has been documented as 1.5-3 months (Littlejohn and Martin 1974), 1-3 months (Williamson and Bull 1992), and 1-2 months (Lemckert 2001). Metamorphs have an average SVL of 9.06 ± 1.0 mm (pers. obs.).

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Chapter 3: Can Life History Studies Contribute to Understanding the Impacts of Clearfell Logging on Pond Breeding Anurans? A Review

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ABSTRACT

Habitat changes resulting from recent clearfell logging in native forests may affect the life history of pond breeding anurans through alterations in the abundance of breeding sites, conditions within breeding sites, terrestrial food abundance, ground surface conditions, terrestrial predation pressure, and forest fragmentation. All these changes have the potential to modify anuran life history traits such as body size, body condition, fecundity, egg size, size at metamorphosis, and duration of the larval period. I review the literature describing these influences and propose that life history studies may provide a novel approach for assessing the effects of forest disturbance on anurans. I argue that this approach to biomonitoring the impacts of logging may provide a constructive complement to population-based approaches that collect abundance and species richness data. Traditional approaches often lead to simplistic 'log or not log' recommendations, whereas life history data could provide a basis for constructive, defensible, alternative

silvicultural practices designed to mitigate unfavourable environmental conditions for amphibians.

Keywords. anuran, bio-indicator, forestry, harvesting, life history, logging.

INTRODUCTION

Informed forest management cannot be undertaken without an understanding of the ecological dynamics of forest ecosystems and the impact of forest disturbance. Due to the complexity of ecosystems, direct measures of all aspects of ecosystem change are too difficult and expensive. Instead, representative components and/or representative processes of systems are selected and monitored as indicators of change, i.e. bio-indicators (Turner and Pribble 1996). A bio-indicator is any organism or group of organisms indicative of a particular environment or set of environmental conditions (Allaby 1985). Bio-indicators can be used as a method of evaluating current management practices or management alternatives.

In this review I discuss how habitat changes resulting from recent clearfell logging in native forests may affect the life history of pond breeding anurans. In keeping with this approach I have structured my comments predominantly from a habitat perspective since a given habitat change may influence numerous life history traits. I propose that life history studies may provide a novel approach by which to identify ecological change associated with logging, thus providing either complementary or alternative approaches

to traditional bio-indicator studies. My focus is on pond breeding anurans, but where helpful I have included examples from the broader amphibian literature.

FROGS AS BIO-INDICATORS

Amphibians have been widely advocated as having greater relative sensitivity to environmental change than other taxa, both within the scientific literature and within the general media (see critique by Pechmann and Wilbur 1994). Several aspects of amphibian natural history suggest that they may be useful bio-monitors of ecosystem health. These include ectothermy, exposure to aquatic and terrestrial environments, restricted home ranges, high philopatry, relatively limited dispersal ability, and the possession of moist, permeable eggs, gills, and skin (Blaustein *et al.* 1994; deMaynadier and Hunter 1995; Tyler 1994).

Penchmann and Wilbur (1994) debated the assertion that amphibians are more sensitive bio-indicators than other species. They argued that the suggestion has not received adequate study and that, to date, no evidence had been presented to support such a claim. However, irrespective of their relative sensitivity, the biology of amphibians may mean that they are valuable indicators of specific types of environmental change that other taxa may be less sensitive to.

RESEARCH ON THE IMPACT OF FORESTRY ON ANURANS

Current understanding of the impacts of logging is limited predominantly to literature from North America. Despite this emphasis on North American ecosystems, it remains

worthwhile to summarise the findings of the review by deMaynadier and Hunter (1995) who concluded that any trends identifiable in the existing literature base were highly variable, within and between studies. Species-specific responses were responsible for much of this variation, the biology of some species predisposing them to greater sensitivity to logging practices than others. Environmental variation within treatments also contributed to variability, further complicating generalisations. DeMaynadier and Hunter (1995) also highlighted deficiencies in the experimental design of many studies, and these limited the capacity to draw definitive conclusions relating to logging treatment. Despite these difficulties, studies examining the short-term effects of clearfelling showed a higher abundance of amphibians in forest control plots than in recently harvested plots, but detected no significant difference in species richness. The regeneration of suitable microhabitats and interspecific differences in colonizing capacity meant that the impact of logging was more variable in the longer term. It should also be remembered that many of the studies reviewed included both salamanders and frogs, and salamanders appear to have a greater sensitivity to logging practices than anurans (deMaynadier and Hunter 1995).

LIMITATIONS OF ABUNDANCE AND SPECIES RICHNESS STUDIES

The literature investigating the impact of forest management on anurans has done so primarily by comparing species abundance and/or species richness. However, anurans are known for their very high diurnal, seasonal, and annual variability in abundance. Annual population fluctuations have been found to vary by factors as large as 10 to 100 fold (Berven 1990; Berven and Grudzien 1990; Blaustein *et al.* 1994; deMaynadier and

Hunter 1995) and the larger the temporal variation in population size, the lower the power of any statistical tests to identify trends due to human impacts (Pechmann and Wilbur 1994). Therefore, dramatic natural population fluctuations can easily obscure, or be mistaken for, anthropogenic declines. Although the reliability of short-term data sets will, largely, be influenced by the life histories of the particular species being sampled (deMaynadier and Hunter 1995), in general, long-term research investment is required to adequately assess anuran abundance (Blaustein *et al.* 1994) (although it must be noted that the assessment of species richness does not necessarily require comparable research effort). The challenge is to separate the high natural variability of anuran populations from change associated with land management.

There are also difficulties with the experimental design of research investigating ecological disturbance relating specifically to forestry. These include obtaining sufficient replicates, high spatial and temporal environmental variability (forest type, elevation, weather during migratory period and age discrepancies between control stands and clear-cut treatments), long time-scales that typically exceed the duration of project funding, and the difficulty in pre-empting logging operations in order to collect pre-treatment data. The logistics of addressing all these issues are so great that the results of many amphibian/logging studies have been compromised and their potential for distinguishing trends relating to the logging treatment is limited (deMaynadier and Hunter 1995).

LIFE HISTORY OF ANURANS

Given the significant resource commitments required for obtaining adequate population abundance and species richness data, these types of studies are likely to be rare. Alternative or complementary methods may help ensure that anurans are represented in our management of forest ecosystems.

Anurans have very flexible life histories (Wilbur and Collins 1973), and the comparison of life history strategies may prove to be an effective and alternative indicator of ecosystem change. Intraspecific variation in life history strategies results from variation in environmental conditions and/or genetic adaptation to environments (van Noordwijk 1989). Genetic adaptation occurs after exposure to longer term, inter-generational changes in environmental conditions but species may also respond to short-term changes in environmental conditions by adjusting phenotypic life history traits. For example, the duration of the anuran larval period is influenced by a range of factors, including food availability, temperature, hydroperiod, predation, and intra and interspecific competition (see review by Alford 1999).

Much anuran research has sought to separate sources of life history variation over long term clinal environmental gradients such as altitude and latitude (Berven 1982b; Berven and Gill 1983; Gollmann and Gollmann 1996; Laugen *et al.* 2002; Merila *et al.* 2000). However, few studies have investigated adjustment in life history traits as a result of short-term, anthropogenically mediated environmental change. In such situations genetic adaptation may be minimal because of the short time scales involved; if so, phenotypic

adjustments of life history traits relating to differences in environmental conditions can be isolated.

Life history theory is based on a number of assumptions and these may permit the use of changes in life history traits as an alternative bio-indicator of environmental change. The first assumption of life history theory is the premise that all organisms aim to maximise fitness within their lifetime. At the most basic level, the primary goal of any organism is to reproduce (Roff 1992) and maximum fitness is achieved when the greatest number of successful offspring is produced within the lifetime of the organism (Bell 1980). However, the fitness that can be attained by an individual is limited by the environment and by the physiological constraints on that organism (Roff 1992). In essence, life history analysis is the study of the tradeoffs between different life history traits (McGinley *et al.* 1987) that allow an organism to maximise fitness within a particular ecological setting. For example, some larval anurans developing in ponds prone to desiccation can reduce the duration of the larval period, thus maximising survival. If the risk of complete pond desiccation is limited, larvae may prolong the larval period to maximise size at metamorphosis.

Life history traits adapt to different environmental conditions through phenotypic plasticity; i.e. the ability of a genotype to produce a range of environmentally dependent phenotypes (Stearns 1989). Life history studies address the interaction of phenotypic traits that determine fitness, e.g. size at metamorphosis is often used as an important indicator of overall anuran fitness because it is correlated with other fitness indicators such as survival (Berven 1990; Goater 1994), adult size (Amezquita and Luddecke 1999;

Berven 1990), body size at first reproduction (Amezquita and Luddecke 1999; Semlitsch *et al.* 1988) and age at first reproduction (Semlitsch *et al.* 1988). Increased adult size may also have consequences for fecundity (Kaplan and Salthe 1979; Ponsero and Joly 1998) and male mating success (Berven 1981; Howard 1980). As a result, size at metamorphosis has been the focus of many theoretical studies of anuran life history.

Life history studies increase our understanding of fundamental anuran biology. Because life history traits respond to varying environmental conditions through phenotypic plasticity, their measurement may also be a useful indicator of environmental heterogeneity. Life history studies may, therefore, prove to be a useful approach for indicating the ecological consequences of land management, in general, and forest harvesting in particular.

POSSIBLE IMPACTS OF FORESTRY ON ANURAN LIFE HISTORY

Other than the mortality of animals during logging and post-logging treatments, there are numerous habitat changes associated with logging activities that may affect anuran life history. The considerations presented below are by no means exhaustive but aim to present a number of initial possibilities for further research.

Increased number of Breeding Sites

Commercial forest management may result in an increase in the amount of standing water within the forest landscape (DiMauro and Hunter 2002). This increases the number of potential breeding sites for anurans. For example, in Tasmania, frog

populations have increased as a result of the additional breeding habitat provided by the construction of fire dams by the Forestry Commission (Taylor 1991). Because the main function of these ponds is to provide water for the management of fire, their value as breeding sites for anurans is incidental. The suitability of these breeding sites for different species is likely to be variable and may depend on characteristics such as pond size (Loman 1988), hydroperiod (DiMauro and Hunter 2002), extent of aquatic vegetation (Hazell *et al.* 2001), adjacent vegetation cover (Hecnar and M'Closkey 1996) and proximity to other breeding ponds (Marsh *et al.* 1999).

The incidental creation of ephemeral breeding sites may also occur as a consequence of logging and logging road construction (deMaynadier and Hunter 1995; DiMauro and Hunter 2002; Packham 1995). Harvest machinery may cause soil ruts with compacted soil and reduced hydraulic conductivity (Wronski 1984), encouraging the pooling of water. Adam and Lacki (1993) documented the frequent use of rut ponds on abandoned logging roads by several species of amphibians in Kentucky. Roadside gutters associated with logging road construction may also result in significant increases in standing water. As many as 11 species of amphibians have been found breeding in road puddles and roadside ditches by T. Pauley in West Virginia (unpublished data: deMaynadier and Hunter 1995).

The effectiveness of smaller ponds as anuran breeding sites is highly dependent on hydroperiod and the duration of the larval period of species that occupy them. Because the ponds are small and often exposed, high evaporation rates may mean that larvae are unable to complete metamorphosis before pond desiccation occurs (DiMauro and Hunter

2002). If pond desiccation is sufficiently delayed to permit metamorphosis, metamorphs are also likely to emerge at a smaller size (Crump 1989) and thus may have reduced survival (Berven 1990; Goater 1994) and adult body size (Amezquita and Luddecke 1999; Berven 1990). Temporal environmental variability may mean that small, ephemeral water bodies are not consistently successful as breeding sites. At those times when conditions are conducive to breeding success (a wetter season, for example), ephemeral standing water may make significant contributions to total reproductive output in the forest landscape.

A higher abundance of standing water, irrespective of its value as a breeding site, may also increase the connectivity between breeding ponds and facilitate increased mobility of anurans within the forest landscape. Pond isolation has been positively correlated with male site fidelity and time to pond colonization (Marsh *et al.* 2000) and negatively with reproductive effort in the tungara frog (*Physalaemus pustulosus*) (Marsh *et al.* 1999). Pond occupancy, rate of colonization and reproductive effort also decreased with distance from breeding site (Marsh *et al.* 1999). Decreased pond isolation may reduce the likelihood of species' extinctions at breeding ponds (Skelly *et al.* 1999).

The availability of reproductive sites may also affect population structure, mating systems and sexual selection. Prohl (2002) found the abundance of tadpole-rearing sites (reproductive resources for female *Dendrobates pumilio* exhibiting significant parental care) to be ten times greater in secondary than primary forest. Population abundance was higher in the secondary forest although, interestingly, the adult sex ratio was more

female biased in secondary forest than in primary forest. As a consequence male mating success and male reproductive success was also greater in secondary forest.

Changing Conditions Within Breeding Sites

Logging may also change conditions within anuran breeding sites. These changes may influence the life history of the egg and larval life stages as well as affecting behavioural choices made by adults such as the choice of oviposition site.

Palik *et al.* (2001) found that shading around ponds increased with time from the logging of the surrounding upland forests. Werner and Glennemeier (1999) and Skelly *et al.* (2002) reported higher water temperatures in ponds with reduced canopy cover, and this observation may significantly influence growth rates of larvae (Hota 1994). Skelly *et al.* (2002), for example, found that temperature differences of 5 °C between open and closed canopy experimental ponds was likely to be the most important determinant of higher larval growth rates in less shaded ponds. It is also possible that reduced shading may also increase the temperature range experienced within breeding ponds and extreme conditions may even result in water temperatures exceeding the thermal tolerance of anuran species.

Increased solar radiation is also likely to increase primary productivity within breeding sites (Batzer *et al.* 2000). Palik *et al.* (2001) found that the abundance of macroinvertebrates that graze on algae correlated negatively with pond shading, indicating increased levels of algal growth as a result of increased solar input. Werner

and Glennemeier (1999) and Skelly *et al.* (2002) found that growth rates of leopard frogs (*Rana pipiens*) and spring peepers (*Pseudacris crucifer*) respectively, were significantly reduced as a result of reduced food availability in closed canopy ponds. Increased quantities of coarse woody debris may also occur within ponds as the vegetation around the pond becomes more established (Palik *et al.* 2001), thus affecting the quality of tadpole food.

Pond shading may also affect pond hydroperiod because a higher incidence of solar radiation may result in increased evaporation and subsequent pond desiccation. The duration of the larval period has often been shown to covary with pond duration (Crump 1989; Newman 1989). For example, Blaustein *et al.* (1999) studied the effect of increased solar radiation on the developmental plasticity of *Hyla savignyi* larvae on north and south facing slopes. They attributed shorter larval periods and smaller metamorphic size to the higher water temperatures and the shorter hydroperiod of less shaded ponds on south facing slopes. An indirect association between pond shading, hydroperiod and pond permanence may also have repercussions on predator abundance. Studies have shown an increase in predator density with pond permanence (Skelly 2001). Skelly (1995b) found that the presence of predators reduced the activity of two species of conspecific tadpoles. This reduced activity resulted in reduced growth rates.

Changes in Ground Surface Conditions

Although anurans show a reliance on wet environments within the forest landscape, the importance of the forest as foraging habitat should not be overlooked (Goldingay *et al.*

1996). For ground-dwelling frogs, the litter layer provides important habitat and clearfelling has been shown to significantly alter litter layer microhabitat components such as coarse woody debris, litter depth, understorey vegetation, canopy closure, moisture, light levels, temperature, and pH (deMaynadier and Hunter 1995; O'Connell 1987; Taylor 1991).

Loss of canopy closure may also decrease relative humidity at the ground level and reduced litter may expose the surface of the ground to increased air movement, thus increasing evaporative water loss and dehydration risk. For animals such as anurans, that show a reliance on moist habitats, even a small reduction in humidity may have negative repercussions for survival. In desiccation experiments by Rothermel and Semlitsch (2002) the water loss of salamanders was significantly greater in open fields than in forests. Bellis (1962) found that the degree and duration of wood frog (*Rana sylvatica*) activity decreased with decreasing humidity. He also found that the average body size of frogs was greater in drier habitats, presumably because larger frogs have a smaller surface area to volume ratio and are, therefore, less prone to dehydration.

Even partial removal of the overstorey by timber harvesting may result in increased insolation leading to higher temperatures on the forest floor (O'Connell 1987; Raymond and Hardy 1991; Vanderwoude and de Bryun 2000). Rothermel and Semlitsch (2002) reported mean above ground maximum temperatures in forest and adjacent fields of 28.3 °C and 39.9 °C respectively, although mean soil temperature and mean relative humidity did not differ significantly. Nocturnal species may be less affected because temperature differences are likely to be moderated at night (Schlaepfer and Gavin 2001). Because

they are ectothermic, the body temperatures of anurans are strongly related to ambient environmental temperatures. Exposure to higher temperatures may lead indirectly to increased dehydration by increasing metabolism and evaporation rates (Bellis 1962). Temperature has also been shown to significantly influence maternal reproductive investment. Female size tends to increase in colder habitats (Berven 1982b) thus leading to a concomitant increase in fecundity (Berven 1982b; Ponsero and Joly 1998; Williamson and Bull 1995). Ambient temperatures experienced during vitellogenesis may also influence egg size with larger eggs being produced at lower temperatures (Kaplan 1987; Williamson and Bull 1995).

Availability of Food in the Terrestrial Environment

Clearfell logging may alter the abundance and assemblages of leaf litter invertebrates and may have consequences for the quality and quantity of food available to anurans. The thickness of the litter layer was considered by Bornemissza (1969) to be the most important factor determining population levels of invertebrates and reductions in the litter layer are likely to follow clearfelling and post-logging burning. Many studies report reductions in the density of many groups of invertebrates as a result of reduced vegetative cover, forest harvesting and fire (Madden *et al.* 1976; Newman 1991; Van Wilgenburg *et al.* 2001; but see Vanderwoude and de Bryun 2000) who found that ant activity and species richness increases immediately following fire in selectively harvested, open forests in South East Queensland).

Changes in invertebrate assemblages following logging may also have consequences for nutritional status because anurans are opportunistic feeders (Tyler 1994) and their diet tends not to reflect specific dietary choices. Lehman (1978) demonstrated significant differences in size of ovaries and oviducts, and mass of livers, fat bodies and final body mass in *Rana pipiens* fed on four different diets (crickets, flies, sowbugs and wax moths).

Nutritional status is likely to affect growth rate and this may have repercussions for time to sexual maturity, adult body size (and its consequences for fecundity and susceptibility to predation and desiccation) and body condition. Seasonal variation in nutritional status has been found to significantly affect egg size and the number of eggs in *Rana tigrina* (Girish and Saidapur 2000) and vitellogenesis within *Bufo bufo* (Jorgensen 1982).

Changes in Terrestrial Predation Pressure

Logging also has the potential to affect the predation pressure on anurans by changing habitat complexity. In the initial post-logging period, reduction in leaf litter and coarse woody debris 'opens up' the forest floor, reducing cover and increasing the exposure of anurans to predators. As the forest regenerates, however, woody debris, litter depth, and understorey vegetation may be at even higher densities than that found within a mature forest.

Heinen (1993) suggested that American toads (*Bufo americanus*) were least susceptible to predation in habitats with a higher density of vegetation and darker soil colour. He

also found that behavioural choices by toads meant that they avoided habitat with reduced complexity. Similarly, Gregory (1983) found that the daytime activity of *Leptodactylus melanonotus* at the pond bank was significantly influenced by the height of terrestrial vegetation. He hypothesised that vegetation structure may influence the time available for feeding and, in turn, may have consequences for individual growth rates and population dynamics.

Logging may also increase the abundance of predators. For example, reptiles may benefit from increased insolation (Greenberg 2001) and the abundance of basking sites such as stumps, logs and roads as a result of forest harvesting. Although not related specifically to forests harvesting, Rothermel and Semlitsch (2002) found snakes (a major predator of anurans) in greater abundances in open agricultural areas than in forest. Similarly, Jaggi and Baur (1999) attributed lower densities of snakes to an increase in the density of trees in the Swiss Jura Mountains. They concluded that logging maintains suitable habitat for these predators by increasing temperatures of microhabitats. Although the availability of such microhabitats may be reduced as forest regeneration occurs, basking sites provided by roads will persist, irrespective of logging phase (Taylor 1991). Because anuran breeding ponds are often constructed adjacent to roads, the importance of road sides as habitats for reptile predators may be especially significant.

Fragmentation of Forests

Because amphibians are restricted physiologically to moist habitats and are relatively poor dispersers compared to other vertebrates (Blaustein *et al.* 1994), the landscape structure between ponds may be an important influence on anuran movement. The commercial forest landscape typically exhibits a patchwork of forest with varying ages. This fragmentation of the forest landscape into different age classes may affect the movement of anurans by altering the resistance of forest landscape.

Empirical evidence relating amphibian movement to habitat is variable and species specific. For instance, avoidance of open canopy conditions was demonstrated for juvenile wood frogs (deMaynadier and Hunter 1999), spotted salamanders (*Ambystoma maculatum*) and American toads (*Bufo americanus*) but not for small-mouthed salamanders (*A. texanum*) (Rothermel and Semlitsch 2002). Roads with heavy traffic significantly increase mortality in amphibians crossing them (Trombulak and Frissell 2000) but forestry roads typically have less traffic and may not exhibit high levels of direct mortality (deMaynadier and Hunter Jr. 2000). Rather, amphibians may avoid forestry roads due to increased predation or desiccation risk. Conversely, the wet margins of road gutters may increase the connectivity of the forest landscape for anurans (deMaynadier and Hunter Jr. 2000).

It is not only the characteristics of the surrounding upland forest but also its proximity to the breeding pond that influences landscape fragmentation and anuran distributions (Guerry and Hunter Jr. 2002). For metapopulations, the proximity of breeding sites to

each other is also a determinant of pond occupancy by different species (Skelly *et al.* 1999) and cannot be separated from investigations of landscape fragmentation.

ASSESSING THE IMPACT OF LOGGING USING A LIFE HISTORY APPROACH

There is some danger that anurans will be inadequately represented in land management planning, precisely because few data justifying management decisions are available (Hazell 2003). Life history studies may provide a novel approach to provide these data, ensuring that this vertebrate group receives adequate consideration in the management of natural resources.

Life history studies relating to forestry are based on the assumption that logging will disrupt existing nutrient and energy pathways. Instead of evaluating differences in population abundance or species richness, life history studies aim to identify differences in phenotypic traits that result from the disruption of these pathways because of logging treatment.

The response of amphibian life history to environmental change has received extensive investigation relating especially to differences in altitude, latitude and climate (for example, Berven 1982a; Berven 1982b; Gollmann and Gollmann 1996; Merila *et al.* 2000). At their most fundamental level, these types of studies make life history comparisons between two or more contrasting environmental conditions. However, the execution of life history studies relating to anthropogenic environmental change (i.e.

recent rather than long-term environmental change) may be simpler than these former investigations because the time scales since environmental change are relatively short and adaptation is unlikely or small. Genetic divergence, therefore, may not always have to be considered.

Any differences in life history with logging treatment are, in themselves, evidence that logging treatments are ecologically distinct. However, to determine if the impacts of logging have a positive or negative effect on species, changes in life history need to be related to a species' fitness.

Assessments of fitness can be made directly (i.e. by measuring differences in survival and/or reproduction) but can also be made by investigating phenotypic traits that are indicators of fitness. For example, Stearns (1992) identified eight principal life history traits related to reproduction and survival: size at birth; growth pattern; age at maturity; size at maturity; number, size and sex ratio of offspring; age and size specific reproductive investments; age and size specific mortality schedules and length of life. By investigating the relationship between fitness and logging treatment we may be able to determine why logging affects populations the way it does, thus deepening our understanding of ecosystem process and function.

The approach may best be illustrated by the following hypothetical example. Monitoring data may reveal that the population abundance of Species A (a species of significant conservation concern) and Species B (an abundant species that is not of current conservation concern) decrease as a result of recent logging. For Species A, life history

research may reveal that decreased shading around breeding sites results in decreased size at metamorphosis and a subsequent reduction in post-metamorphic survival that is independent of the terrestrial environment. The larval life history of Species B is not similarly affected by pond shading but, rather, the species is unable to recolonise ponds that are surrounded by recent clearfelling because logging increases the resistance of the landscape to the species' movement. Life history studies also show that migration patterns of Species B are affected for only a limited period until a threshold density of understorey vegetative structure regenerates. While both species are negatively affected by recent logging, the reasons are distinct and the appropriate management response also varies. The impacts of logging on Species A may be simply mitigated by prescribing a vegetative buffer around suitable breeding sites. For Species B management may recommend vegetative corridors linking upland forest to breeding sites until the surrounding vegetation is sufficiently regenerated so as not to impede movement. But, because this species is of little present conservation concern, the short-term, localized effects of logging may not significantly impact the overall population abundance on a landscape scale. As a result, management prescriptions may rather rely on natural regeneration of understorey over time.

It is evident from the above example, that life history studies may be able to provide explicit data illuminating why fitness is reduced. This is in contrast to most monitoring programs that have provided only limited data relating to the reasons for population decline. As a result previous management recommendations have been restricted predominantly to whether logging should be excluded from an area or not. The management recommendations derived from life history studies, however, may be

broadened to include alternative silvicultural practices that can mitigate unfavourable environmental conditions for amphibians. In this way, conflict between wood production and conservation may be reduced in multiple use forests.

Therefore, life history studies investigating land management, and logging in particular, have great potential on two counts. Firstly, they may be a useful complement to traditional studies as they may provide ecological explanations for differences in abundance and species richness exhibited by monitoring data; i.e. life history studies may explain why the effects of logging are species specific, which particular life stage is affected (i.e. egg, tadpole, adult) and, why effects vary with forest type and alternative logging practices. Secondly, life history studies may provide alternative ways to measure the impact of logging on anuran populations in their own right.

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Chapter 4: Breeding Site Characteristics Regulating Life History Traits of the Brown Tree Frog, *Litoria ewingii*

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ABSTRACT

Past research has determined the habitat requirements of amphibian species predominantly from presence/absence studies. This study tested the hypothesis that relationships between breeding site habitat components, life history traits and fitness may provide a higher resolution of biological data relating to the habitat requirements of amphibian species. We tested this novel approach by using *Litoria ewingii* as our model species. We correlated larval and metamorph life history traits with habitat variables at twenty-eight small to medium sized ponds within a commercially logged forest in southern Tasmania, Australia. To avoid larval mortality due to pond desiccation, *L. ewingii* laid eggs and metamorphosed earlier in smaller ponds. Snout vent length at metamorphosis increased with elevation and metamorphosis was earlier in less shaded ponds. Breeding ponds that maximised the fitness of *L. ewingii* were higher elevation ponds with reduced shading, steeper bank slopes and reduced pond isolation. The findings of the study equip land managers with a greater ecological understanding of ecosystem function in relation to specific species. The methodological approach has

broad application to conservation biology where an awareness of the specific habitat requirements of amphibians is critical to successful ecosystem management.

INTRODUCTION

The availability and suitability of breeding sites is an important influence on a species' distribution and, therefore, is also an important determinant of population abundance and conservation status. This is especially true for amphibians whose dual aquatic and terrestrial life stages typically demand concomitant landscape complexity. Habitat factors required by amphibians are often interrelated and several, concurrent habitat components may be required in and around a water body for it to be suitable as a breeding site.

Past research has determined the habitat requirements of pond breeding amphibian species predominantly from studies of presence/absence. Such studies have shown that habitat requirements are highly species specific and that a multitude of habitat conditions directly influence the presence of amphibians. For example, breeding site suitability is influenced by size (Loman 1988; Vos and Chardon 1998), permanence (Skelly *et al.* 1999), mean annual temperature (Hazell *et al.* 2001), water quality (Hecnar and M'Closkey 1996; Rowe and Dunson 1993), extent of aquatic vegetation (Hazell *et al.* 2001) and shading (Skelly *et al.* 1999; Werner and Glennemeier 1999).

Likewise, components of the surrounding landscape may be determinants of breeding site use. Species assemblages at breeding sites may be influenced by the percentage of

the surrounding area with native tree cover (Findlay and Zheng 1999; Hazell *et al.* 2001) and percentage of disturbed forest in a selectively harvested commercial forest landscape (Lemckert 1999). The proximity of other breeding ponds and limitations in dispersal ability have also been shown to restrict distribution (Baker and Halliday 1999) and the intensity of breeding at ponds (Marsh *et al.* 1999).

Of the multitude of landscape scale studies investigating the habitat requirements of amphibians, few have attempted to measure the relationship between breeding site habitat components, life history traits and fitness of amphibians (for exceptions see Rowe and Dunson 1993). Arguably this type of approach may provide as much or more information about the habitat requirements of species when compared to presence/absence studies because a higher resolution of biological data is provided.

We tested this novel approach by using *Litoria ewingii* as our model species. Despite the fact that *L. ewingii* is an abundant species, its basic habitat requirements and preferences remain unstudied. Because *L. ewingii* is a habitat generalist, factors limiting breeding site selection are likely to be few and traditional studies investigating species presence/absence are not likely to reveal much about its biology. To contend with such a broad range of different habitat conditions, however, the species may make adjustments to its life history. Investigations of life history traits may, therefore, enable the characterisation of *optimal* breeding sites (i.e. those with the most successful reproductive output) in place of a categorical judgement of breeding site suitability provided by presence/absence data.

The specific aims of our study were to collect basic life history data for *L. ewingii* and to correlate life history traits with breeding site characteristics by measuring larval and metamorph life history traits and habitat variables at twenty-eight small to medium sized ponds within a commercially logged forest of southern Tasmania, Australia. Ultimately, we wished to assess the value of this approach as a method for determining the habitat requirements of amphibians in order to broaden the conservation management tools available to land managers.

DESCRIPTION OF SITE STUDIED

The study site is centred on the commercially harvested forests of the WARRA Long Term Ecological Research (LTER) site, Tasmania, Australia (43°3'S; 146°39'E). Vegetation at the site consists predominantly of temperate broad leaf forest (mainly *Eucalyptus obliqua* wet forest), with the remainder of the area consisting of moorland, alpine vegetation, temperate rainforest, riparian forests, coniferous forest and scrub (Brown *et al.* 2001). The site has an average annual rainfall of 1080 mm (Hickey *et al.* 2001). Precipitation falls throughout the year but average monthly rainfall and the number of storms show a strong winter bias, with the highest rainfall occurring during July and August (Ringrose *et al.* 2001).

MATERIALS AND METHODS

The Study Species

Litoria ewingii (commonly known as the brown tree frog) is a medium sized frog with an adult snout vent length of up to 45 mm (Robinson 1996). It is widely distributed throughout south-east Australia and is abundant at the study site. Breeding occurs predominantly during spring, but limited breeding may also occur during autumn. In Tasmania the species breeds in both permanent and ephemeral standing water and lays up to 450 eggs per clutch (B. Lauck, unpublished data). Eggs are laid in clustered jelly masses attached to vegetation within the pond. The tadpoles are active swimmers (Martin and Littlejohn 1982) with a larval period of approximately 1.5-7 months (Sokol 1984; Tyler 1994). *Litoria ewingii* is sympatric with one other amphibian species at the study site, *Crinia signifera*. Niche partitioning for larvae of the two species is expected to be strong (Peterson *et al.* 1992) and little interspecific interaction is expected since *C. signifera* tadpoles are largely benthic and *L. ewingii* utilises the entire water column (Peterson *et al.* 1992).

Measurement of Breeding Site Habitat Components

A total of twenty-eight small to medium sized permanent ponds have been constructed adjacent to roads at the study site. These are used as water supplies for the purposes of fire management by Forestry Tasmania. These ponds provide mostly permanent, incidental breeding sites for amphibians. They exhibit a range of habitat conditions and nearly all have been colonised by *L. ewingii*. We initially included all twenty-eight

ponds in the study; however, not all ponds were included in final analyses due to pond destruction, pond alteration, and pond drying (see results for the number used in each analysis).

The bathymetry of each pond was defined using two water depth transects within each pond and the subsequent conversion of these point data to 10 cm interval contour data using the spline function in ArcView™ GIS. Pond volume, surface area, maximum depth, % pond < 10 cm deep and bank slope were calculated from the resulting digital maps. The amount of bare pond substrate was also digitised onto these maps and recorded as a percentage of the total pond substrate.

Pond productivity was estimated by suspending microscope slides at the water surface for 2 weeks (with 3 temporal replicates) within each pond and measuring the amount of organic matter deposited on the surface of the slide (adapted from Skelly 1995a). The slides were protected from herbivory by placing them in gauze envelopes. Upon removal from the pond, each slide was dipped in formalin to stop further algal growth and then dried in the laboratory. Once dry, they were weighed (±0.001 mg) and placed in a 500 °C muffle furnace to combust all organic matter. When cooled the slides were re-weighed and the difference in mass (i.e. amount of organic matter) was taken as an indication of primary productivity.

Distance to the nearest established forest, distance to nearest pond, and elevation were derived from the relevant GIS data layers provided by Forestry Tasmania. Pond age was

estimated by personnel from Forestry Tasmania (pers. comm. Bob Schuecker). Ponds were classed as shaded if vegetation greater than 2 m in height was located within one metre of the pond bank or if any vegetation was overhanging the pond bank.

Attempts were made to sample predatory pond invertebrates using an artificial substrate method (Bennison *et al.* 1989). Unfortunately this methodology did not successfully trap predators. This may have been due to their low density or because the traps did not provide an appropriate substrate for the predator species present. As a result, predator effects could not be included in the study. No fish species occurred in any of the ponds.

Leaf litter invertebrates (i.e. density of potential frog food) were sampled from 3x0.33 m^2 haphazardly located litter samples from terrestrial locations around the pond margins and extracted using Tulgren funnels (see Ananthakrishnan 1996). The dietary preferences of *L. ewingii* are unknown. Therefore, the total number of invertebrates at each site was recorded, irrespective of taxonomic classification.

Measurement of Life History Traits

All ponds were visited fortnightly for a period of seven months (September 2000 to March 2001) for the collection of life history data. At each visit, each pond was surveyed for the presence of eggs. The density of clutches could not be measured since *L. ewingii* lays clutches of eggs in jelly masses distributed in separate clumps within a pond.

Tadpoles were sampled using funnel traps (Richter 1995). Two funnel traps were installed in each pond (one at the surface of the water and the second on the substrate of the pond). Traps were installed initially for a period of 24 hours; however, towards the end of the season the density of tadpoles meant that traps would fill up completely within this time, creating anoxic conditions and tadpole asphyxia. Consequently, from December onwards, traps were installed for a period of two hours only. Tadpoles were removed from the traps using a small net and placed on a white tray together with a 30 cm metal ruler (which was used as a reference length). A digital photograph was taken of the tray. Number of tadpoles and tadpole SVL were subsequently measured from these photographs. Tadpoles were returned immediately to the pond.

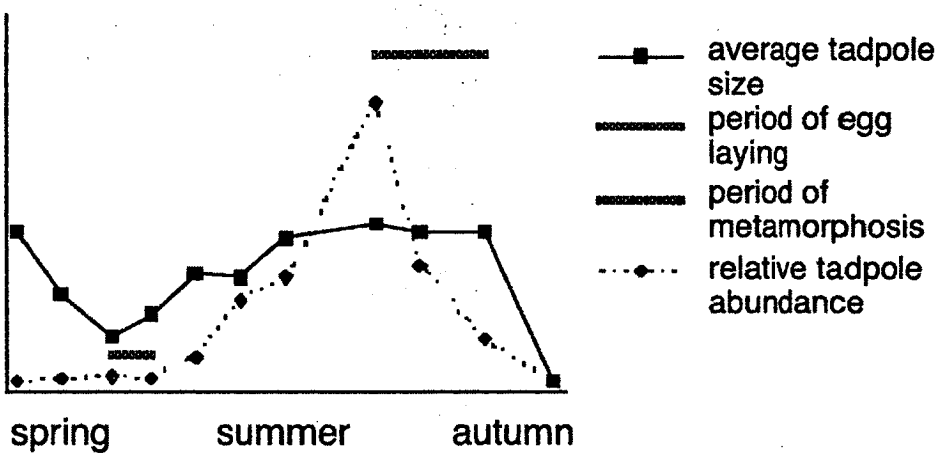
The average of the number of tadpoles caught in surface and bottom traps and divided by trap time gave an estimate of relative tadpole abundance. Because tadpoles exploit microhabitats within the ponds, these data were seen as coarse estimates of tadpole relative abundance only.

Metamorphs were hand captured around the banks of each pond. Mass (±0.05 g) and SVL (snout vent length, ±0.05 cm) were measured at the site of capture and the animals released immediately. Metamorphs that had not quite reached Gosner (1960) stage 46 were returned to the laboratory, measured the following day and released at the natal pond upon subsequent field trips.

Summary life history data were calculated for each pond (see Figure 10 for a diagrammatic description of typical data). A reference starting date at the beginning of spring (1 September 2000) was used for many of the calculations. The period of egg laying was calculated from the date when eggs were first present in ponds to the date when eggs last appeared (days). First hatching was calculated as the date when small size class tadpoles (<10 mm) were first present in ponds (days since 1 September 2000); Last hatching was calculated as last date when small size class tadpoles were present in ponds (days since 1 September 2000). The period of hatching was calculated as the number of days between first and last hatching. Maximum relative abundance was the maximum relative abundance of tadpoles caught in funnel traps, unadjusted for pond volume. The maximum number of tadpoles was calculated on the date that maximum relative abundance occurred by multiplying maximum relative abundance by pond volume. Duration of larval development was calculated as the number of days between the middle of the hatching period and the middle of the metamorphic period. The median (50^{th} percentile) and 90^{th} percentile tadpole size was calculated from tadpole SVL data on the date at which maximum relative abundance occurred. First metamorphosis was calculated as the number of days from 1 September 2000 to the date at which metamorphs were first detected. Last metamorphosis was calculated as the number of days from 1 September 2000 to the date at which metamorphs were last detected. Period of metamorphosis was calculated as the number of days between first and last metamorphosis. Mass of metamorphs was calculated as the average mass of all metamorphs captured at the site. SVL of metamorphs was calculated as the average SVL

of all metamorphs captured at the site. The timing of metamorphosis was calculated as the number of days from 1 September 2000 and the middle of the metamorphic period.

Figure 10. Diagrammatic example of life history data collected for each pond



RESULTS

Statistical analysis was undertaken using SPSS™ 8.0 for Windows Student Version. α was defined as 0.1 because of the non experimental nature of the study and because the sampling intensity required to measure life history traits necessitated small overall sample sizes (deMaynadier and Hunter 1995).

Three ponds were severely disrupted by earthworks during the course of the study and two further ponds were destroyed during the later stages of the study period. Four ponds dried before metamorphosis began. Because most disruptions occurred later in the season, some life history data could be collected for all ponds but complete sets of data for ponds were limited.

General life history of L. ewingii

Egg laying was detected between 20 September 2000 and 15 November 2000. Eggs may have been present but not detected outside this peak period of egg laying due to their low density. Egg laying also coincided with the presence of tadpoles in smaller size classes. Such data indicated that limited egg laying also occurred in December and January. Laying during this period occurred in two ponds only. Autumnal egg laying did not occur, probably because of the low rainfall experienced at the site during the autumn of 2001 (some autumnal laying was observed in the following, much wetter autumn of 2002 (pers. obs. B. Lauck)).

Larvae were found throughout the year. In some ponds all larvae metamorphosed within one season, but in others over-wintering of larvae occurred. It was not possible to ascertain if over-wintering larvae were from clutches laid in the previous spring or autumn.

Metamorphs were detected between 29 November 2000 and 7 March 2001. This was taken as the peak period of metamorphosis as it coincided with a drastic drop in the density of tadpoles within ponds. Two metamorphs were also incidentally detected in early spring, presumably having overwintered as tadpoles.

Relationships between life history variables

We used linear regression to test the relationships between amphibian life history traits that were chosen *a priori* to be biologically meaniful. Before regressions were conducted, all life history variables were assessed for high pair-wise correlation, curvilinear relationships, leverage and influence, by visually inspecting pair-wise scatter plots. Results of regression analysis are presented in Table 1.

Table 1. Results of linear regressions between life history variables

Parameters	r^2	*d.f.*	*F*	*P*
90th percentile tadpole size versus metamorph SVL	0.433	1,12	5.350	0.054
90th percentile tadpole size versus metamorph mass	0.387	1,8	4.411	0.074
Maximum relative abundance of tadpoles versus metamorph mass	0.273	1,10	3.375	0.099
Maximum relative abundance of tadpoles versus metamorph SVL	0.184	1,9	2.034	0.188
Larval period versus metamorph mass	0.556	1,9	10.001	0.013
Larval period versus 90 percentile tadpole SVL	0.313	1,13	5.468	0.038
Larval period versus metamorph SVL	0.015	1,8	1.210	0.737
Metamorphic Period versus maximum number of tadpoles	0.189	1,16	6.077	0.021
CV 90th percentile tadpole size versus hatch period	0.063	1,21	1.410	0.248
CV 90th percentile tadpole size versus length metamorphic period	0.166	1,16	4.177	0.054
CV 90th percentile tadpole size versus maximum number of tadpoles	0.239	1,13	4.077	0.065
CV 90th percentile tadpole size versus larval period	0.270	1,16	5.557	0.032
CV 90th percentile tadpole size versus 90th percentile tad size	0.000	1,21	0.005	0.943

The 90th percentile of tadpole SVL was positively related to SVL at metamorphosis but no significant relationship was found between the 50th percentile tadpole size and SVL

at metamorphosis. The maximum relative abundance of tadpoles in ponds was negatively related to mass at metamorphosis but not SVL at metamorphosis. The duration of the larval period significantly influenced the mass of metamorphs, with mass increasing as larval period increased. Larval period was negatively related to the 90th percentile SVL of tadpoles but not to SVL at metamorphosis. The period of metamorphosis was positively correlated with the maximum number of tadpoles found in ponds. Although not used in the subsequent analyses with pond habitat variables, the variation in tadpole size was positively correlated with the duration of metamorphosis and the 90th percentile tadpole size, and negatively correlated with larval period.

Principal components analysis of habitat variables

The sampling strategy resulted in a small number of ponds, a large number of pond habitat variables and insufficient degrees of freedom with which to sensibly conduct multiple regressions (Hero *et al.* 1998; Stumpel and van der Voet 1998). Principal component analysis (PCA) with Varimax rotation was undertaken to group habitat variables into related components that explained the majority of variance in pond habitat characteristics. This effectively increased the ratio of pond to habitat variables and thereby increased the degrees of freedom in subsequent analysis.

Principal components analysis reduced the twelve pond habitat variables to four components that explained 76.8% of the total variance of the original variables (Table 2). Groupings of variables within components were biologically sensible. The variables within component 1 were related to pond proportions with high PC values relating to

large, deep ponds with large surface areas and low PC values relating to small, shallow ponds with small surface areas. The variables in component 2 related to pond shape and its repercussions on in-pond vegetation. High PC values denote ponds with steep banks, a small area of shallow water and large area without a vegetative substrate and low PC values denote ponds with a large area of shallow water, a large area of vegetation covering the pond substrate and a gradually sloping bank. High PC values also denote a shorter distance to the nearest pond. The variables in component 3 were related to the condition of pond waters. High PC values denote younger ponds with high primary productivity and low shading and low PC values denote older ponds with more established vegetation and lower primary productivity. The variables within component 4 were related to the surrounding terrestrial habitat. High PC values denote uncleared vegetation with a high abundance of litter invertebrates and low values denote logged sites with low abundance of invertebrates. The only variable within a component which appeared unrelated to co-grouped variables was the 'distance to closest pond' variable within the 'pond shape' component.

Table 2. Rotated component matrix resulting from principal components analysis of pond habitat variables (Varimax rotation with Kaiser Normalisation)

Habitat Variable	Component			
	1	2	3	4
Pond surface area	0.961			
Pond volume	0.946			
Maximum depth	0.666	0.575		0.206

Habitat Variable	Component			
	1	2	3	4
% surface area < 10cm deep	0.205	-0.860		
Bank slope		0.765	0.376	
% bare substrate		0.703		-0.389
Distance to the closest pond	-0.207	-0.562	0.480	
Pond productivity		0.305	0.891	
Pond age	0.437		-0.757	
Pond shading	-0.266		-0.635	0.217
Terrestrial invertebrate density				0.887
Type of surrounding vegetation	-0.327		0.435	-0.612
Total Variance Explained (%)	27.1	23.9	15.3	10.5

PCA scores were retained for subsequent multivariate analysis with amphibian life history traits. Elevation was classed as a 5th, separate habitat component of interest.

Relationship between habitat variables and amphibian life history

Principal components analysis, by definition, produces 'components' that are statistically independent, thus negating collinearity of independent variables in subsequent multiple regressions. Stepwise multiple regressions were undertaken using the 5 pond habitat components (scores for the first four principal components 4 PCA plus elevation) with each amphibian life history trait. The α value for entry into the model was defined as 0.1 and removal as 0.15. The results of analyses are summarised in Table 3.

Table 3. Results from stepwise multiple regression between habitat components and individual life history traits

Life History Trait	PCA Habitat Component	R^2	*d.f.*	*F*	*P*
90th percentile tadpole SVL @ maximum relative abundance	3 (pond water)	0.268	1,11	3.666	0.085
50th percentile tadpole SVL @ maximum relative abundance	3 (pond water)	0.315	1,11	4.604	0.057
SVL of metamorphs	Elevation	0.391	1,7	3.860	0.097
Maximum of tadpoles	2 (pond shape) & elevation	0.244	2,22	3.224	0.061
Last hatching	-	-		-	-
Maximum relative abundance	-	-		-	-
Period of hatching	-	-		-	-
Mass of metamorphs	-	-		-	-
First hatching	1 (pond proportions)	0.192	1,15	3.324	0.090
Larval period	-	-		-	-
Timing of metamorphosis	1 (pond proportions) & 3 (pond water)	0.783	2,10	14.455	0.002
Period of metamorphosis	-	-		-	-
Last metamorphosis	1 (pond proportions)	0.439	1,10	7.051	0.026
First metamorphosis	1 (pond proportions)	0.583	1,10	12.604	0.006

DISCUSSION

Past studies have often identified the habitat requirements of amphibians by measuring the presence/absence of species at breeding sites but, for ubiquitous species such as *L.*

ewingii, such studies reveal little information. In this study we investigated the correlation between different habitats and suites of life history traits to reveal new information about the biology of the species and its ability to adjust to spatially variable environmental conditions. We discuss the significance of our findings in the context of existing experimental life history theory in order to determine the types of breeding sites that maximise the fitness of *L. ewingii*. Finally, we assess this type of experimental design as a novel management tool to describe the habitat requirements of amphibians.

General life history of L. ewingii

At the study site, *L. ewingii* bred in both permanent and temporary ponds. Day-time calling was heard between September and February, and night-time calling was evident throughout the year. Calling intensity and frequency were highly dependent on rainfall (pers. obs. B. Lauck). In the 2000/2001 seasons, egg laying took place predominantly during spring, with limited amounts of laying in early summer. During the following season, very limited autumnal breeding was also observed. Lack of laying in the autumn of 2001 may be attributed to the dry conditions experienced in that season, as the autumn of 2002 was significantly wetter and evidence of some breeding activity was found.

In the spring of 2001, large, overwintering larvae were present in nine out of 28 ponds. The disappearance of these tadpoles by the middle of spring (October) and the observation of two metamorphs at this time indicate that overwintering larvae do not delay metamorphosis to coincide with the peak metamorphosing period in summer.

Early metamorphosis of overwintering larvae may maximise fitness by reducing the desiccation risk that metamorphs are exposed to later in summer and by reducing intraspecific competition during the peak periods of metamorphosis. Overwintering larvae may also develop into larger metamorphs due to their longer developmental time in colder temperatures. Larger size at metamorphosis and metamorphosis early in the season have both been shown to maximise subsequent adult fitness traits in other species (Amezquita and Luddecke 1999; Berven 1990; Semlitsch *et al.* 1988; Williamson and Bull 1996). Overwintering larvae may therefore have a competitive advantage over larvae that complete their development within one season provided that a longer exposure to in-pond predation does not negate this advantage.

The duration of the average larval period at the site was 46 days (S.E.= 13.5). This compares with the findings of Sokol (1984) who reported a larval period of 1.5-2 months for *L. ewingii* tadpoles maintained at a temperature of 19-21 °C. Our data also indicate that it is possible for metamorphosis to be reached in less than one month, which is much shorter than other documented larval periods which reported 6-7 months (Martin and Littlejohn 1982).

Relationships between life history variables

The 90th percentile tadpole size was found to be a good predictor of the average SVL at metamorphosis. A similar relationship between median tadpole size and SVL at metamorphosis did not exist, showing that early (as opposed to later) larval growth is not a determinant of metamorphic characteristics. This finding is consistent with that of

Alford & Harris (1988), who found that the early growth period had little influence on final metamorphic parameters in *Bufo woodhousei fowleri*. A lack of relationship between median tadpole size and SVL at metamorphosis may also indicate that size at metamorphosis may differ for those tadpoles metamorphosing later in the season; however, temporal sampling intensity was insufficient to investigate this possibility.

The relationship between 90th percentile tadpole size and the mass of metamorphs was not as strong as that between 90th percentile tadpole size and SVL, indicating that mass at metamorphosis was more variable than SVL. Instead, the relative abundance of tadpoles in ponds was found to be a significant determinant of mass at metamorphosis. The relationship between metamorphic size and intra/interspecific competition is well established: smaller size at metamorphosis correlates with increased density and an associated increase in competition for resources (Smith-Gill and Berven 1979; Sokol 1984; Wilbur and Collins 1973). However, similar results have also been documented when resources are not limiting. Alford (1999) identified a number of mechanisms that may result in negative correlation between growth rate and density in environments with unlimited resources; these included behavioural or social stress, fouling of water with metabolic waste, production of or infestation with parasites that increase with density, and production of inhibitory chemical substances. Sokol (1984) showed that *L. ewingii* tadpoles raised at higher densities in laboratory conditions had slower growth rates, longer larval periods and were smaller at metamorphosis. He also conducted a partition experiment which showed that diffusable factors rather than social or behavioural stress were responsible for these changes in life history traits. Interestingly, in our study SVL

at metamorphosis and duration of the larval period were not influenced by tadpole density. Relationships between duration of the larval period and size at metamorphosis are highly variable and dependent upon temporal variations in larval conditions (Alford and Harris 1988). For example, Travis (1984) predicted a positive relationship between larval period and metamorphic size when there are increasing or constant resources within a pond and *vice versa*. Without specific experimental analysis, the mechanisms influencing the covariation of these life history traits cannot be further isolated for *L. ewingii*.

The duration of larval development was found to be a good predictor of 90th percentile tadpole SVL but no similar relationship was found between SVL at metamorphosis and the time spent as a larva. However, the significant relationship between 90th percentile tadpole size and SVL at metamorphosis indicates that we should expect larval period to affect size at metamorphosis and low degrees of freedom may be responsible for failure to identify a relationship. 90th percentile tadpole size was found to decrease as larval period increased. This indicates accelerated developmental rates (i.e. reduced larval period) at the expense of metamorphic size. Such plasticity in life history traits by tadpoles indicates an avoidance of hostile in-pond conditions in preference for the terrestrial environment.

The duration of the period over which metamorphosis took place at each pond was strongly related to the maximum number of tadpoles in the pond. During the period when metamorphosis was occurring, the size of tadpoles remaining in the pond was also

more variable in ponds with the largest numbers of tadpoles. This high variability in size was not correlated with the length of the hatching period, showing that tadpoles hatching at different times and developing for different lengths of time did not cause variability. Gromko *et al.* (1973) found that variability in tadpole size was greatest in high density conditions for *Rana pipiens*. High tadpole numbers (as opposed to high densities) may trigger similar mechanisms that influence growth rates. Alternatively, the relationship between the length of the metamorphic period and the maximum number of tadpoles in the pond may be an artifact of sampling method rather than amphibian life history. Larger numbers of metamorphs emerging from a pond may mean that the researcher is more likely to encounter them. Total larval survival was highlighted by Berven (1990) as a chief factor determining adult recruitment and warrants further study.

Relationship between habitat variables within Principal components

The ponds available to *L. ewingii* as breeding sites encompassed a wide range of different pond habitat conditions and our choice of sample sites was based on the inclusion a full range of these conditions. Principal components analysis grouped existing habitat variables into four components that explained 77% of the overall variation. The first two components explained the majority of this variation (50%) with 15 and 10% of the total variation being explained by the third and fourth components, respectively.

The relationships between habitat variables in Principal component 1 (pond proportions) are relatively self-explanatory since ponds of greater volume are likely to have larger

surface area and a greater maximum depth. This component may have important implications for amphibian life history in terms of pond hydroperiod and pond microhabitats, both of which may influence behavioural decisions made by adult amphibians in relation to breeding site choice (Loman 1988). Rowe & Dunson (1993), for example, found egg deposition in spotted salamanders (*Ambystoma maculatum*), was positively correlated with pond volume. Other studies have shown that some species have a competitive advantage in ponds with a shorter hydroperiod and *vice versa* (Skelly 1995b; Skelly 2001) and that reduced hydroperiod can induce amphibian larvae to accelerate development in order to metamorphose before pond desiccation occurs but at a smaller size (Crump 1989). Specific laboratory studies indicate that *L. ewingii* may not be restricted to a particular depth microhabitat but typically uses the entire water column (Peterson *et al.* 1992).

Principal component 2 grouped habitat variables that delineated pond shape and its consequences for emergent and non-emergent vegetation. As pond banks become steeper the proportion of shallow water decreases. Shallow water is usually considered the productive zone of the pond because solar radiation is able to penetrate to the pond substrate. Consequently, ponds with a steep slope and a smaller area of shallow water also typically have a greater percentage of the pond that is devoid of emergent and non-emergent vegetation. Studies have demonstrated habitat partitioning by amphibian larvae based on the amount of vegetative cover (see review by Alford 1999). Habitat complexity may reduce the incidence of predation by reducing encounters with predators and may also reduce physical encounters with conspecifics, thus mediating density

effects on life history. Pond shape may also influence temperature gradients within ponds and temperature is an important influence on larval period and size at metamorphosis (Berven *et al.* 1979). Larvae may, for example, behaviourally select warmer pond microhabitats (Noland and Ultsch 1981) to accelerate development, thus reducing the duration of the larval period.

Principal component 3 encompassed variables that influenced pond water conditions. There was a significant negative relationship between pond age and productivity with shaded ponds being more likely to have low levels of productivity. As ponds age, the vegetation around the pond margins becomes more established (Palik *et al.* 2001). This increased shading is expected to reduce the amount of solar radiation entering ponds, thus reducing algal growth. Werner & Glennemeier (1999) and Skelly *et al.* (2002) found that growth rates of leopard frogs (*Rana pipiens*) and spring peepers (*Pseudacris crucifer*), respectively, were significantly reduced as a result of reduced food availability in closed canopy ponds. Pond shading may also affect water temperature with larvae developing more rapidly but emerging at a smaller size at higher temperatures (Skelly *et al.* 2002). Manually collected surface water temperature data indicate that mean water temperatures in ponds at the study site were similar but that maximum temperatures were attained sooner and were almost six degrees higher in unshaded ponds thus effectively exposing tadpoles in these ponds to warmer waters throughout their development (B. Lauck, unpublished data).

Principal component 4 described the terrestrial environment surrounding ponds. The terrestrial environment may affect movement to, and colonisation of, a pond by adult amphibians and consequently may affect breeding intensity at the pond. The hostility of the terrestrial environment may also affect the survival, health and reproductive output of adult amphibians. For example, variations in litter invertebrate density (i.e. food availability to adults) may affect in-pond life history by influencing body condition of, and reproductive investment by, adults.

Relationship between pond habitat components and amphibian life history

The results of multiple regression between life history traits and habitat components showed that SVL at metamorphosis increased with increasing elevation. It is well established that temperature varies systematically with altitude (Berven *et al.* 1979) and that amphibian larvae growing slowly due to low temperature regimes at higher altitudes metamorphose at a larger size than do larvae reared at higher temperatures (Berven *et al.* 1979; Smith-Gill and Berven 1979).

Egg laying and first hatching occurred earlier in smaller ponds indicating that *L. ewingii* has the ability to adjust behaviour associated with mating and egg laying in order to facilitate maximum survival of the larvae. Smaller ponds have a greater risk of premature desiccation and earlier breeding will maximise the chances of tadpoles reaching metamorphosis before ponds dry in summer. Even though four ponds did dry before metamorphosis could take place, data relating to the timing of metamorphosis did indicate that metamorphosis was both initiated and completed earlier in smaller ponds.

Timing of metamorphosis and size of tadpoles (both 90th percentile and 50th percentile SVL) was influenced by water conditions within the ponds. Time to metamorphosis decreased and the size of tadpoles increased in less shaded ponds. Reduced shading has been shown to increase both pond productivity and water temperatures due to an increase in received solar radiation (Skelly *et al.* 2002; Werner and Glennemeier 1999) and the variations in life history traits found in this study are consistent with experimental manipulation of food abundance and temperature (Alford and Harris 1988; Berven 1982b).

The relationship between the maximum number of tadpoles, elevation and pond edge/isolation characterististics may have been influenced by behavioural breeding site choices made by adult amphibians. Increased pond isolation has also been shown to decrease breeding intensity at ponds by the tungara frog, *Physalaemus pustulosus* (Marsh *et al.* 1999). Because both pond edge and pond isolation characteristics were grouped into the same principal component it was not possible to separate these effects. However, given the relationship between tadpole numbers and metamorph numbers (as discussed above), and the importance of larval survival for populations (as highlighted by Berven 1990), isolating the mechanisms behind breeding intensity warrants further investigation.

The well established positive relationships between metamorph size, the timing of metamorphosis and adult fitness (Amezquita and Luddecke 1999; Berven and Gill 1983;

Semlitsch *et al.* 1988), and metamorph number and adult population size (Berven 1990) allow us to determine the type of pond which maximises fitness in *L. ewingii*. When making such inferences about fitness, however, it is important to make the distinction between fitness of individuals and fitness of the population as a whole. Commercial harvesting activities have undoubtedly led to an increase in overall population fitness by increasing the abundance of *L. ewingii* within the landscape. This is predominantly due to the incidental construction of breeding sites that would not have been available had the landscape not been commercially logged. On a smaller scale, the greatest number of tadpoles *per pond* was exhibited by higher elevation ponds and ponds with steeply sloping banks, small areas of shallow water, and limited vegetation covering the pond substrate.

Although unintentional, differences in the construction of ponds have also resulted in different breeding site characteristics and these, in turn, influence the fitness of individuals emerging from them. Our study has shown that larger metamorphs are likely to emerge from younger ponds with less established vegetation, whose reduced shading is not likely to limit primary productivity and tadpole food. Larger tadpoles also emerged from ponds at higher elevations, presumably due to the exposure of larvae to colder temperatures and consequently prolonged development (Berven *et al.* 1979; Smith-Gill and Berven 1979).

Shading also influences the timing of metamorphosis. Early metamorphosis has been associated with increased fitness by initiating the movement of juveniles into terrestrial

habitats at more benign times (Berven and Gill 1983; Williamson and Bull 1996), thus increasing adult fitness (Semlitsch *et al.* 1988). Earlier metamorphosis in ponds with reduced shading may mean that metamorphs are not initially exposed to the drier summer conditions that are more common later in the season. Earlier metamorphosis may also mean that juveniles increase the time that they can forage (to maximise growth and build fat reserves) before a less active period over the winter months.

The early metamorphosis that was evident from smaller ponds does not necessarily confer an increase in fitness because of the higher desiccation risk associated with this type of pond. Complete desiccation may result in total larval mortality from a pond but even partial pond drying may confer reduced fitness to larvae that can complete metamorphosis through reduced metamorphic size (Blaustein *et al.* 1999). Smaller ponds are more likely to be successful breeding sites during wetter, cooler seasons whereas larger ponds provide more reliable habitat irrespective of annual climatic variability.

In short, breeding ponds that maximise the fitness of *L. ewingii* are higher elevation ponds with reduced shading and steeper bank slopes.

An Assessment of the Experimental Approach as a Tool for Determining Habitat Requirements of Amphibian Species

Before assessing the advantages of this approach, we would like to note a couple of limitations. Firstly, although the study allows us to delineate pond conditions that

maximise the fitness of amphibian larvae and metamorphs, it does not consider the effect of the surrounding terrestrial landscape upon the fitness of later life stages and therefore, only allows qualified inferences about these life stages. The terrestrial habitat provides foraging habitat, shelter from predators, refuge from desiccation and a landscape through which individuals must move in order to forage and disperse. For example, changes in vegetation structure resulting from land management practices such as logging (as may be the case at our particular study site), may significantly alter many adult life history traits that, in turn, may have important consequences for fitness.

Secondly, it is also important to note that, although they typically provide greater ecological resolution, single species studies have limitations in that they do not consider the habitat requirements of sympatric species. *Crinia signifera* was sympatric with *L. ewingii* at all our study ponds and niche partitioning and behaviour diverge significantly for the larval life stage (Peterson *et al.* 1992). Consequently, the breeding site habitat requirements that maximise the fitness of *C. signifera* may be significantly different to those of *L. ewingii*. Conflicting habitat requirements will undoubtedly complicate land management recommendations.

Despite these limitations, our study successfully describes the flexible life history strategies of *L. ewingii* that enables this species to colonise a range of breeding sites exhibiting different conditions. The study was able to characterise the type of breeding site that maximises the fitness of *L. ewingii*.

The findings from the experiment provide biological resolution that would not otherwise have been obtained from the presence/absence approach and equip land managers with a greater ecological understanding of the commercially harvested wet forests of south-eastern Tasmania. This type of information would be especially valuable to conservation biologists wishing to determine the true availability of breeding sites to specific species of conservation concern. The approach may also be used to explain species range declines where previous studies have not been able to identify causality. Furthermore, the approach may facilitate population recovery for species exhibiting population declines as a result of habitat degradation by allowing conservation biologists to create appropriate artificial habitat.

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Chapter 6: The impact of recent logging and pond isolation on pond colonization by the frog *Crinia signifera*

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ABSTRACT

A colonization experiment was used to investigate landscape use of a commercially managed wet forest in Southern Tasmania by the ground-dwelling frog, *Crinia signifera.* Replicated artificial ponds were placed at increasing distances (20, 100, 250 and 500 m) from nine permanent breeding sites to investigate the effect of pond isolation on colonization. To investigate the effect of recent logging on colonization, four of these permanent breeding sites were surrounded by coupes that had been logged within the previous five years and five permanent breeding sites were surrounded by unlogged forest. The rate of colonization, the frequency of colonization, male size and female size (inferred from clutch size) were monitored over two breeding seasons. No pond isolation effects were found, indicating that *C. signifera* is distributed widely throughout the forest landscape for up to 500 m around each permanent breeding site. Such patterns of forest habitat use indicate that management prescriptions should not only take into account the habitat characteristics of breeding sites but should also consider the surrounding terrestrial landscape. Ponds surrounded by unlogged forest were colonized

almost two times faster than ponds surrounded by logged forest indicating that landscape modification can significantly alter amphibian mobility. These findings have consequences for total reproductive output especially in landscapes where breeding sites are highly variable and for species that are slow to colonize new breeding sites.

Keywords: colonization, fragmentation, forest management, frogs, logging, ponds.

INTRODUCTION

Anthropogenic fragmentation of ecosystems at a landscape scale have been a matter of recent ecological concern, chiefly because habitat fragmentation may act as a barrier to the movement of many species. Reduced colonization and increased extinction has been found with increasing distance between discontinuous habitat patches (Saunders *et al.* 1991). These problems are especially important for species with population sizes that are influenced or even regulated by rates of immigration (Driscoll 1997). In addition to repercussions on population dynamics, such barriers to movement may also result in changes in sex ratio, age structure, social dynamics, and genetics of populations (deMaynadier and Hunter 1995; Driscoll 1997). The effects of habitat fragmentation may be exacerbated when breeding habitats are variable in space and time (Marsh *et al.* 1999).

Because they are generally slow moving and small bodied, amphibians have low mobility compared to other tetrapods (Blaustein *et al.* 1994). As a result of their permeable skin they are also constrained to remain near moist refugia. These

physiological restrictions may mean that amphibians are particularly susceptible to land management practices, such as logging, which drastically alter the local landscape through which they may forage and disperse. Clearfell logging followed by post-logging burning significantly alters the amount of woody debris, litter depth, understorey vegetation, canopy closure, moisture and pH (see review by deMaynadier and Hunter 1995). Such changes could increase landscape resistance to amphibian movement by changing factors such as food abundance and desiccation and predation risk. At the same time, however, logging and logging road construction may incidentally increase the abundance of pooled water (e.g. as a result of soil compaction from harvest machinery and road gutters) and this may reduce the distances that pond breeding amphibians need to travel to breeding sites by increasing the density of standing water within the forest landscape (DiMauro and Hunter 2002). In turn, this could increase the connectivity between populations, effectively reducing fragmentation of amphibian habitat. The findings of Marsh *et al.* (1999) confirm that pond isolation and habitat factors may act inter-dependently to determine patterns of breeding pond use.

Although habitat changes as a result of logging may not necessarily change the resistance of the landscape to the movement of populations, they may do so for individuals. For example, Ponsero and Joly (1998) found that distance moved by *Rana dalmatina* through 'non-habitat' is positively correlated with size while Bellis (1962) found that the average body size of frogs was greater in drier habitat, presumably because larger frogs have a smaller surface area to volume ratio and, therefore, are less prone to dehydration.

To investigate factors affecting the mobility of amphibian species within a commercially managed forest landscape I conducted a pond colonization experiment in which I investigated both the effect of recent logging and the effect of breeding pond isolation on the colonization of artificial ponds. I wished to determine if these factors influenced the rate and/or intensity of colonization, and to establish if colonization was size dependent, since size is an important determinant of reproductive investment.

The experiment was based on the premise that, other factors being equal, the time to colonize new ponds will increase with the resistance of the landscape and increasing migration distance. Does logging significantly increase the resistance of the landscape (at least in the short term) to amphibian movement? If so, larger frogs may be better able to colonize logged habitats than smaller frogs (Ponsero and Joly 1998) and relative reproductive output may consequently be increased. Due to their reduced susceptibility to desiccation and predation, larger frogs may also be more capable of migrating greater distances.

My aim was to evaluate this experimental approach as a means of studying the impact of land management on small, cryptic amphibian species. I used the common brown froglet (*Crinia signifera*) as my model species. *Crinia signifera* is a small ground-dwelling frog with an adult snout vent length range of 20-30 mm. Breeding in Tasmania occurs predominantly during early spring and summer (with autumnal breeding less common). The species is a generalist, is found in a wide range of habitats and is not excluded by logging. Eggs are laid singly, attached to substrate at the bottom of the pond and clutch sizes of up to 500 eggs have been noted in Tasmania (pers. obs).

METHODOLOGY

Study Area

The study site is centred within the commercial forests of the WARRA Long Term Ecological Research (LTER) site, Tasmania, Australia (43°3'S; 146°39'E). The site has an average annual rainfall of 1 080 mm (Hickey and Neyland 2000). Precipitation falls throughout the year but average monthly rainfall and number of storms show a strong winter bias, with highest rainfall occurring during July and August (Ringrose *et al.* 2001). Vegetation at the site consists predominantly of temperate broad leaf forest (mainly *Eucalyptus obliqua* wet forest) and logging and fire history at the site has resulted in a full range of successional stages of this forest type (www.warra.com). The remainder of the area consists of moorland, alpine vegetation, temperate rainforest, riparian forest, conifer forest and scrub (Brown *et al.* 2001). Standard logging practices in wet schlerophyll and mixed forests at the site consist of clearfell, burn and aerial sowing with eucalypt seed on a rotation of 90 years (Hickey and Neyland 2000).

Fieldwork

Medium sized, permanent ponds have been constructed adjacent to roads as water supplies for the management of fire by Forestry Tasmania in August 2001. These ponds provide incidental, permanent breeding sites for amphibians at the study site. Nine permanent ponds (4 surrounded by recently logged (i.e. < 5 years) and 5 by unlogged

coupes) were chosen from the total number of ponds in the landscape. Only ponds located at least one kilometre from other permanent ponds were accepted.

Four artificial ponds were constructed at distances of 20, 100, 250 and 500 m from each of these permanent breeding ponds. To avoid frogs using the artificial ponds as 'stepping stones' for the colonization of other artificial ponds, they were placed so that they were further from each other than from the permanent breeding pond (Marsh *et al.* 1999). The dimensions of each artificial pond were 1.0 x 0.8 x 0.3 m. The inside of each pond excavation was lined with layers of newspaper, as protection against sharp rocks or sticks, beneath a 2 x 2 m sheet of UV light resistant clear plastic. The edges of the plastic were buried under soil and/or rocks and logs. Each pond was filled using water collected at a nearby river crossing; this ensured that no amphibian eggs or larvae were inadvertently introduced, since no Tasmanian frog breeds in rivers. Due to the logistics of filling artificial ponds with water, they were all constructed within 30 m of forest roads. This consistency removed roads as a confounding factor in analyses. Substrate from the surrounding area and small branches were placed in the bottom of the pond to provide an egg laying substrate.

The experiment was conducted from August 2001 to February 2003. Each artificial pond was monitored weekly during the peak egg laying period in August to December for the presence and number of clutches. During summer and autumn monitoring was reduced to a 2-weekly or monthly frequency. At each visit, all eggs were removed from the pond (so that intraspecific competition did not influence pond colonization) and returned to the laboratory for the measurement of clutch size. In order to do this, individual clutches

were placed on a white plastic tray so that individual eggs were spread out in a single layer and could be differentiated from one another in a digital photograph taken of the whole tray. When two or more clutches at different stages were present, three close-up photographs were taken in order to determine the proportion of eggs at each stage. Clutch size was then calculated by extrapolating the proportion of eggs at different stages in the close-up photos, to that of the whole tray.

At each field visit, the immediate area around each pond was also hand searched for adult *C. signifera*. Snout-vent length (SVL) was recorded for all captures. The black and white belly patterns of *C. signifera* are unique to each frog and digital photographs served as a method of identification for individual frogs.

The experimental design assumed that the availability of other breeding sites did not confound the experiment. To test this assumption I also measured the amount of standing water along two 60 m transects centred on each artificial pond and located perpendicular to one another. The first transect was directed along roadside gutters and the second into the surrounding forest. The total length of standing water and the amount of standing water suitable as breeding habitat that intersected each transect was recorded.

Statistical Analysis

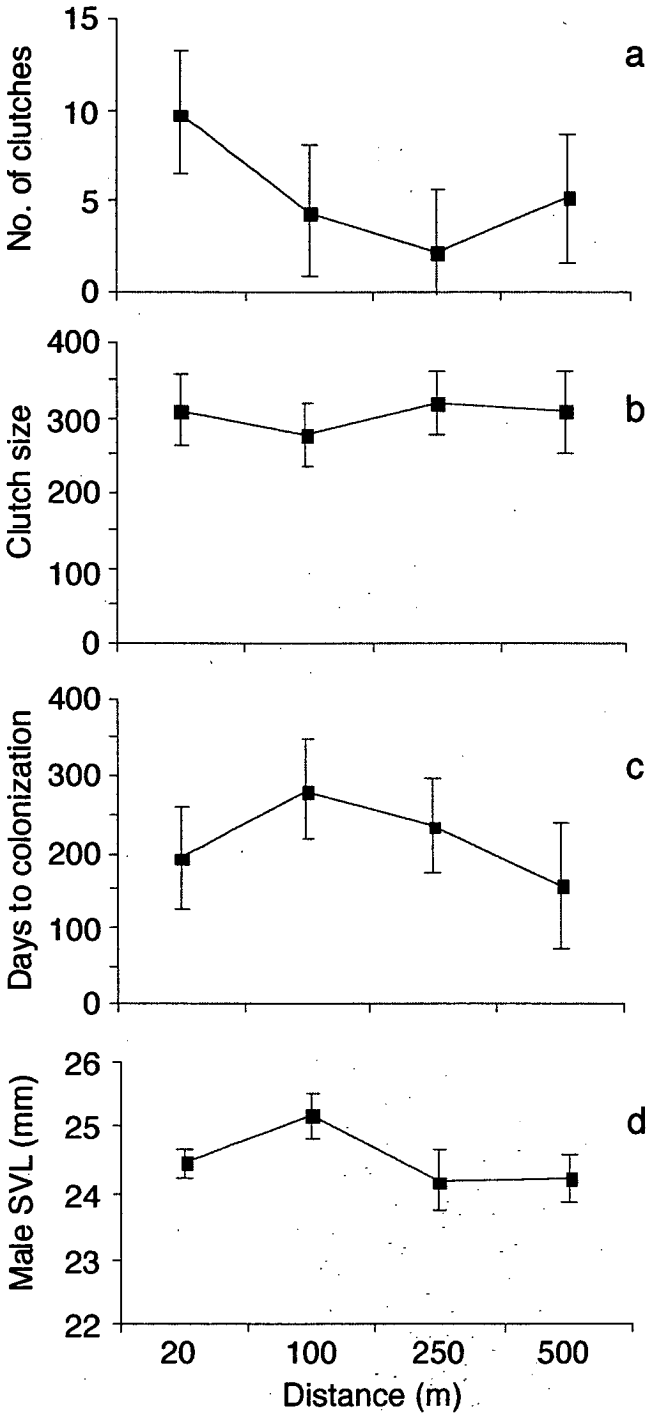
Because of damage to 4 artificial ponds during the course of the experiment, the initial split plot experimental design (with the logging treatment the between plots variation

and the distance treatment the within plots variation) was unbalanced, with insufficient residual degrees of freedom. As there was no evidence of a distance effect (see results), distance data were pooled and nested ANOVA was used to investigate any differences in time to colonization, number of clutches and mean clutch size with logging treatment. Nested ANOVA was also used to compare SVL of males with logging treatment. Kolmogorov Smirnov tests were used to test differences in the amount of standing water and breeding habitat along roadside gutters and within the forest between logged and unlogged sites. Assumptions for all statistical tests were confirmed and no transformation of data was required.

RESULTS

Mean number of clutches, clutch size, the rate of colonization and male size did not differ with pond isolation (Figure 12).

Figure 12. Mean and standard error of a) number of clutches, b) clutch size, c) number of days till colonization and d) male body size (SVL) at artificial ponds in relation to distance from the permanent pond.



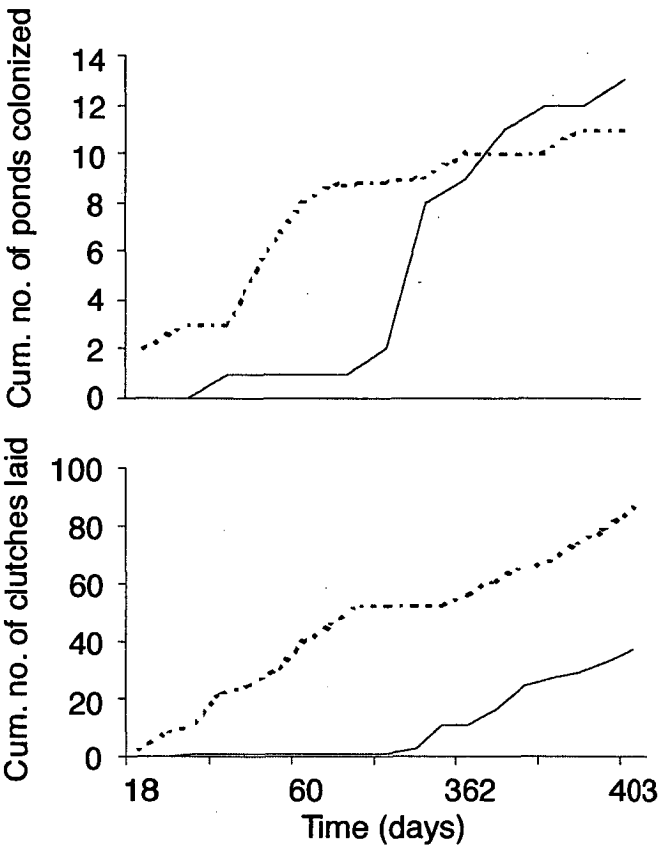
Although the number of clutches per pond and the mean clutch size did not differ significantly between logging treatments, ponds surrounded by unlogged forest were colonized twice as fast as those surrounded by logged forest (115 ± 45.8 days compared to 331 ± 37.4 days respectively) (Table 10). The SVL of males from unlogged sites was greater than that from logged sites (26.0 ± 0.36 mm and 24.1 ± 0.27 mm, respectively) (Table 10).

Table 10. Influence of logging treatment on colonization of ponds by *C. signifera*

Dependent Variable	d.f.	*F*	*p*
Number of clutches	1,25	2.414	0.133
Mean clutch size	1,16	2.348	0.145
Days to first colonization	1,16	13.339	0.002
Male size (SVL)	1,106	16.106	< 0.001

The total number of ponds colonized at the end of two breeding seasons was the same (Figure 13a) but the total number of clutches laid in ponds surrounded by unlogged forest was almost double that in ponds surrounded by recently logged coupes because they were colonized sooner (Figure 13b).

Figure 13. Cumulative number of a) ponds colonized and b) clutches laid in ponds over time by *C. signifera* at ponds surrounded by unlogged forest (dashed line) and harvested forest (solid line)



The total amount of standing water was greater within the logged forest than the unlogged forest (4.2 and 2.4 / 60 m, respectively). Of this standing water, only a fraction was suitable as breeding sites for *C. signifera*. The amount of standing water suitable for breeding did not differ between logging treatments (Table 11).

Table 11. Difference in the abundance of standing water with logging treatment

Dependent Variable	Asymp. sig.
All standing water within the forest	0.001
All standing water along roadside gutters	0.452
Standing water within the forest suitable for breeding	0.997
Standing water along roadside gutters suitable for breeding	1.000

DISCUSSION

Studies investigating the impact of logging upon amphibians are rare, especially outside North America. As a consequence, these important forest ecosystem vertebrates have received little specific consideration in land management planning. Previous studies investigating the impact of logging on amphibians have done so predominantly by measuring abundance and species richness. However, an understanding of how amphibians use the forest landscape is also crucial for the sustainable management of commercial forests as this identifies the importance of different habitat components, the extent of the landscape used by species, and the impact of forest harvesting upon the movement and connectivity between populations.

Recently, colonization experiments have been undertaken to investigate population structure and forest landscape utilization by amphibians (Johnson and Semlitsch 2003; Marsh *et al.* 1999; Marsh *et al.* 2000; Ponsero and Joly 1998). This experimental approach is particularly appropriate for cryptic pond breeding species such as *C. signifera*.

Pond Isolation

I found that the distance from the permanent pond (pond isolation) did not influence the rate at which artificial ponds were colonized. This indicates that *C. signifera* are dispersed widely throughout the forest, since, if permanent ponds are regarded as founder sites following each breeding episode, it is clear that frogs do not necessarily remain in their immediate vicinity. Dispersal must occur for distances of at least 500 m. This reasoning is supported by the observation that the number of clutches laid in ponds was also independent of distance from the permanent pond. My findings differ from those of Marsh *et al.* (1999) who found that time to pond use by tungara frogs (*Physalaemus pustulosus*) was greatest for ponds furthest from active breeding sites and that the number of egg masses per pond decreased with pond isolation.

Mean clutch size was also unrelated to distance from the permanent pond, indicating that colonization was not correlated with female size. Likewise adult male size did not differ with distance from the permanent breeding site. Since empirical evidence suggests that larger frogs may be able to travel greater distances (Ponsero and Joly 1998), the absence of these size differences in *C. signifera* suggests that dispersal was not physiologically restricted by the forest habitat within the ranges studied.

Overall, my results suggest that 500 m is well within the dispersal range of *C. signifera* over a 2 year period since no isolation by distance effects are evident at this scale. Indeed, four individuals were captured at more than one pond over the two year period, having travelled distances of up to 600 m. Isolation effects may have been evident had

the range of pond distances been increased. Unfortunately, however, the high density of permanent ponds within the study site precluded testing this.

My experimental evidence allows me to make some inferences about the population structure of *C. signifera* in commercial forest landscapes. Average and maximum distances between permanent ponds at the study site were 0.8 and 2.4 km, respectively. This density of permanent ponds is typically much greater than for forest not primarily managed for logging since the majority of these ponds are anthropogenically constructed as part of the forest management process.

Because connectivity between populations at permanent breeding sites is likely to be high, the typical metapopulation structure so commonly associated with pond breeding amphibian populations may not apply in commercial forests such as those in this study. For amphibians, a metapopulation structure can be characterized by isolated breeding populations that become extinct and are then re-established over time. This results in a highly dynamic temporal presence/absence profile of breeding activity across individual breeding sites in the landscape. As a result only a fraction of available, suitable breeding ponds is inhabited at any one time. In contrast, all permanent ponds at my study site simultaneously contained actively breeding populations of *C. signifera* (pers. obs.).

Logging

Although distance from the permanent pond did not influence the rate of pond colonization by *C. signifera*, unlogged sites were colonized almost twice as fast as

recently logged sites. In an experimental investigation of juvenile amphibian dispersal, Rothermel and Semlitsch (2002) also found that spotted salamanders (*Ambystoma maculatum*) moved almost four times further and toads (*Bufo americanus*) almost three time further into forest than into more open fields; these authors concluded that forest habitat provided less resistance to amphibian movement.

Males from unlogged sites were larger than those from recently logged sites and this itself may account for the faster colonization of artificial ponds in unlogged sites, as larger frogs may be able to move faster. Larger frogs may also be able to exploit drier conditions (Bellis 1962) because they have a smaller surface area to volume ratio and therefore, may be mobile during drier periods that smaller frogs are unable to exploit for dispersal. Mean clutch size did not differ between recently logged and unlogged sites indicating that female size also did not differ. Female size may, however, be a less important influence on rate of colonization since male colonization and consequent calling may be the major mechanism influencing dispersal by females. If calling occurred early at ponds surrounded by unlogged forest, for instance, then evidence of colonization (i.e. egg laying) would also have occurred earlier.

It is unlikely that differences in abundance (i.e. numbers of potential colonizers) or oviposition site choices influenced the rate of colonization since neither the intensity of colonization nor the total number of clutches was correlated with logging treatment.

Ecological and Management Implications of Experimental Findings

Although the impact of land management on amphibian populations engenders considerable conservation interest and concern, within Australia this has not so far stimulated much scientific research (Hazell 2003). My study addresses fundamental gaps in our understanding by investigating how frogs used the modified landscapes that result from forest harvesting. Without such data it is unlikely that amphibians can be inadequately represented in land management planning. *Crinia signifera* is an excellent model species for this purpose because it is not excluded by logging (Kavanagh and Webb 1998; Lemckert 1999; pers. obs.). Indeed, its abundance has almost certainly increased as a result of commercial forest management, due to the anthropogenic construction of additional breeding sites (Taylor 1991). These factors ensured that my study was not compromised by small sample sizes.

Although *C. signifera* must rely on the immediate habitat around ponds during the breeding season, my research shows that it does not necessarily remain within this limited area during the remainder of the year, but disperses widely throughout the forest for distances of at least 500 m. Although dependent upon the life history of individual species, land management decisions relating to amphibians should, therefore, not necessarily be limited to the narrow margins surrounding breeding sites.

My study also found that ponds surrounded by unlogged forest were colonized more quickly than those surrounded by recently logged coupes. Although it is possible that this may be due to differences in timing of breeding with logging treatment, there

seemed no difference in the timing and intensity of breeding with logging treatment at permanent breeding sites (see Chapter 7; although this was not quantified in any way).

Even though the final number of ponds colonized in two breeding seasons was the same, the total number of clutches laid in ponds surrounded by unlogged forest was almost double that in ponds surrounded by recently logged coupes (earlier colonization effectively constituted an extra season in which ponds surrounded by unlogged forest contributed to total reproductive output).

Findings such as these have even greater significance for species that depend on ephemeral breeding sites: harvesting, road construction and forest regeneration all increase the uncertainty associated with these sites. Because of their limited lifetime, reproductive success will be significantly influenced by both their availability and the rate at which they can be colonized.

Finally, when generalizing from my findings it must be remembered that not all species can colonize ponds as quickly as *C. signifera* and may, therefore, not be as responsive to the dynamic ecosystems that are produced by forest harvesting. For example, my unpublished results show that *Litoria ewingii*, a widely distributed and abundant frog within Tasmania, is much slower to colonize the same artificial ponds. During the study period, only 25% of ponds colonized by *C. signifera* were also colonized by *L. ewingii,* independent of logging treatment.

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Chapter 7: Logging affects maternal reproductive investment and offspring life history traits in the frogs *Litoria ewingii* and *Crinia signifera*

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ABSTRACT

We isolated environmental effects on maternal reproductive investment in *Crinia signifera* (Girard, 1858) and *Litoria ewingii* (Dumeril & Bibron, 1841) by examining differences in egg size from logged and unlogged sites where genetic divergence is unlikely due to the short time scales since logging (less than 5 years). We also investigated the consequence of differences in maternal investment for offspring life history. We collected eggs from ponds located in either logged or unlogged forest and raised the ensuing tadpoles to metamorphosis under common laboratory conditions. Egg size was greater at unlogged than logged sites for both species. For *L. ewingii*, size at hatching was also greater at unlogged sites; but for *C. signifera* size at hatching was independent of logging treatment. For both species survival at various life stages was greater in offspring originating from smaller eggs at logged sites: for *L. ewingii*, survival to metamorphosis was greater at logged sites despite there being no correlation between survival at hatching and logging treatment; for *C. signifera* survival at metamorphosis

did not differ with logging treatment despite greater survival at hatching in eggs from logged sites. Our findings indicate that land management practices can significantly alter amphibian life history. Increased maternal investment in egg size did not necessarily confer increased fitness for subsequent life stages in the particular experimental larval environment tested. Rather, it is likely that other forms of reproductive investment such as egg quality and paternal contributions may be more significant determinants of offspring fitness.

Key words: egg size, environmental effects, fitness, land management, metamorphosis, survival, tadpole.

INTRODUCTION

Land management practices such as logging alter ecosystems dramatically by changing microhabitat parameters such as the availability of coarse woody debris, litter depth and type, canopy closure, moisture and pH (deMaynadier and Hunter 1995). These alterations to habitat may have repercussions upon amphibian life histories, especially with regard to the reproductive investment of resident breeding adults.

For females, reproductive investment is affected by the genetic makeup of the female, by the environment that she is exposed to throughout her development, and the environment that she is exposed to throughout gamete development (Kaplan 1987). However, few studies have isolated the influence of environmental effects on maternal reproductive investment and amphibian life history (for notable exception see Kaplan 1987).

In this study we isolated the influence of environmental effects on maternal reproductive investment by examining differences in life history traits in amphibians from different environments where genetic divergence is unlikely due to the small time frames involved We investigated the impacts of recent forest harvesting upon egg size (an important estimate of maternal reproductive investment (Parichy and Kaplan 1995)) by collecting eggs from ponds located within either logged or unlogged forest.

The short time scales since logging in our experiment (less than five years) and the fact that *C. signifera* can live for up to seven years (B. Lauck, unpublished data) mean that maternal investment is unlikely to be genetically adapted with respect to logging treatment. In cases where the genetic component can largely be discounted, differences in maternal investment can be used as an indicator of environmental heterogeneity.

Differences in egg size may also have fitness consequences for offspring (Parichy and Kaplan 1992); however, there is growing evidence indicating that egg size is not necessarily the only or most important parental effect determining offspring fitness. Rather, other types of reproductive investment such as egg quality and paternal contributions may also be significant determinants of offspring fitness (Laugen *et al.* 2002; Williamson and Bull 1989). To determine the influence of egg size on subsequent life history traits we hatched eggs collected from logged and unlogged treatments and raised the ensuing tadpoles under common laboratory conditions. We undertook the study using two common anuran species, *Litoria ewingii* and *Crinia signifera,* to determine if responses were species specific.

METHODOLOGY

The study area was centred on the commercial forests of the WARRA Long Term Ecological Research (LTER) site, Tasmania, Australia (43°3'S; 146°39'E). Forests at the site consist predominantly of temperate broad leaf forest (mainly *Eucalyptus obliqua* wet forest). The logging and fire history at the site have resulted in a full range of successional stages of this forest type (www.warra.com). Other types of vegetation include moorland, alpine vegetation, temperate rainforest, riparian forest, conifer forest and scrub (Brown *et al.* 2001). Standard logging practices in wet and mixed forests at the site consist of clearfell, burn and aerial sowing with eucalypt seed on a rotation of 90 years (Hickey and Neyland 2000). Forestry Tasmania has constructed medium sized, permanent ponds adjacent to roads as water supplies for the management of fire. These ponds provide incidental breeding sites for amphibians.

We selected nine permanent ponds (four surrounded by logged and five by unlogged coupes) in which populations of both *L. ewingii* and *C. signifera* occur naturally. Eggs were collected from ponds at weekly intervals between 21 August 2001 and 25 November 2001. Although not quantified, there seemed no difference in the timing and intensity of breeding with logging treatment and samples were assumed to represent the peak breeding period at each treatment. Because sampling was limited to the short, two month peak breeding period at the beginning of the breeding season, it is probable that all clutches collected were the first for the season. Consequently, we consider it unlikely

that energy expenditure devoted to previous clutches would affect provisioning to the eggs we collected.

Litoria ewingii lays its eggs in non-contiguous jelly masses attached to vegetation within the pond. Egg masses of *L. ewingii* were classed as being from separate clutches if they were at different developmental stages or from widely separate parts of the pond. There was a lower certainty that eggs of *C. signifera* belonged to the same clutch because the species lays eggs singly, attached to pond substrate. Eggs of *C. signifera* were classed as belonging to the same clutch if they were found in close proximity to one another and at the same developmental stage. Multiple sampling separated by weekly intervals also increased the likelihood of sampling separate clutches.

Eggs considered to be from the same clutch were placed in separate plastic containers and transported to the laboratory over ice to prevent in-transit mortality and rapid egg development in the warmer weather that occurred later in the season.

Williamson and Bull (1989) showed that most *C. signifera* tadpoles developed abnormally after hatching at extreme temperatures of 4-5 °C or 29 °C. Laboratory conditions were therefore maintained at 17 °C with a photoperiod of 12:12 hours. Water was sourced from a river near Hobart that has a pristine catchment above the point of water collection.

In the laboratory, a sample of three eggs was haphazardly selected from each clutch; each egg was placed in a separate 700 mL plastic container filled to a depth of 5 mm

with water. Egg size (excluding the capsule) was measured at a magnification of x 40 under a binocular microscope fitted with an eyepiece micrometer. Stage was noted (Gosner 1960) and size variations with stage were accounted for by using stage as a covariate in subsequent analyses. Eggs were not utilized in the experiment if stage upon return to the laboratory was greater than nine (as the initial spherical shape becomes distorted after this stage). Loosely fitting lids covered each container.

Hatching date was noted and snout vent length (SVL ± 0.05 mm) at hatching was measured at a magnification of x 35 under a binocular microscope fitted with an eyepiece micrometer. After hatching the water volume of the container was increased to 500 mL and six drops of feeding solution were place in each container. Feeding solution consisted of 10 g high protein baby breakfast cereal per 200 mL of water. Each container was cleaned and water replaced at weekly intervals. Six drops of feeding solution were placed in each container after cleaning.

To identify any temperature microclimates within the laboratory, ten containers with equal quantities of water were place haphazardly throughout the laboratory. Thermochron ibutton™ temperature loggers (produced by Dallas Semiconductor) were programmed to take hourly, simultaneous temperature readings. One logger was placed in each container for a period of 24 hours. All loggers were then placed in the same container for 24 hours to calibrate them against one another. ANOVA (1 way, model 1) indicated that temperatures varied by as much as 2.5 °C at different locations within the laboratory ($F_{1,220} = 602.360$, $P = < 0.001$). As a result, a subset of containers that housed experimental animals were haphazardly relocated to different areas within the laboratory

at three-day intervals throughout the experiment, so that microclimate differences in temperature did not confound experimental results.

At stage 42 (i.e. emergence of both front legs) the water volume within the container was reduce to 50 mL and the container angled on the laboratory bench so that metamorphs did not drown and could easily exit the water. Upon metamorphosis (i.e. complete resorption of the tail at stage 46), date was noted; SVL was measured with calipers (± 0.05 mm) and mass was measured using an electronic balance (± 0.005 mg).

For *L. ewingii*, high mortality occurred between stages 42 and 46 (73% of animals). Consequently, metamorphosis was classed as having taken place at stage 42 instead of 46. To test the correlation between size at stage 42 and 46, 30 later developmental stage tadpoles were collected from a pond at the study site. Regression of size at stage 42 against that at stage 46 was highly significant, confirming that measurements of laboratory animals at stage 42 were meaningful and that comparisons between the two species was valid (n = 30 tadpoles; for SVL: $r^2 = 0.597$, $F_{1,26} = 38.493$, $P < 0.0001$; for mass: $r^2 = 0.925$, $F_{1,26} = 321.613$, $P < 0.0001$).

Upon completion of the study, metamorphs were released to their maternal pond.

Statistical Analysis

Statistical analysis was undertaken using SPSS™ 10.0 for Windows Professional Version. $\alpha = 0.05$ for all analyses. Since individuals from a clutch were not statistically

independent, we removed this nested component by calculating the average of all eggs within clutches and basing further analyses on these summarised data. Williamson (1995) found seasonal differences in egg size for *C. signifera.* We accounted for any similar effects by including the month in which eggs were laid as a source of variation in statistical analyses.

Both species exhibited abnormalities during both the tadpole and metamorph stage. *Crinia signifera* metamorphs exhibited bloated bodies in 44% of cases and hind leg abnormalities in 34% of cases. Thirty nine percent of *L. ewingii* tadpoles exhibited bent tails. Although no definite reason could account for these abnormalities, consultation with other laboratories highlighted lack of sunlight, inadequate diet or temperature differences as the most likely cause (pers. comm. Marion Antis, Reinier Mann, David Newell, Deborah Pergalotti, Jacquie Recsei, Karen Thumm, John Wilkinson). To evaluate the influence of abnormalities, continuous data were analysed using three way, model I ANOVA with the following variables: logging treatment, abnormality and month. Presence of abnormality did not significantly affect any life history trait and was, therefore, removed in further analyses.

Data were reanalysed using two way, model I ANOVA to test for correlations with logging treatment and month. The interaction term between logging treatment and month was insignificant in all cases and was removed in order to increase degrees of freedom in analyses. We used egg stage as a covariate in all egg size analyses as a way of accounting for the influence of in-pond conditions before egg collection and because egg size itself varies with egg stage (King and Kaplan 1997; Williamson and Bull 1989).

We used linear regression to investigate relationships between life history traits. Assumptions for ANOVA tests and regression analyses (i.e. normality, homoscedacity, etc) were confirmed for all data before analysis. It was necessary to log transform mass at metamorphosis and duration of the larval period for *L. ewingii*, and SVL, mass at metamorphosis and duration of the larval period for *C. signifera*. Categorical data were analysed using Kolmogorov-Smirnov two-sample tests with logging treatment or month of oviposition as the grouping variables.

RESULTS

The results from ANOVA analyses examining the effect of logging treatment and month of oviposition on life history traits are presented in Table 12. Results from linear regressions between life history traits are presented in Table 11. The results from Komorgorov-Smirnov two-sample tests examining the effect of logging treatment and month of oviposition on categorical life history traits are presented in Table 14.

Table 12. Results from ANOVAs examining the effect of logging treatment and month of oviposition on life history traits

Dependent Variable	Source of Variation	*C. signifera*			*L. ewingii*		
		d.f.	*F*	*P*	*d.f.*	*F*	*P*
Egg size	Month of oviposition	1,50	0.189	0.666	1,79	0.168	0.658
	Logging Treatment	1,50	4.517	0.039	1,79	14.283	< 0.001
	Stage (covariate)	1,50	3.663	< 0.001	1,79	22.443	< 0.001
Hatch size	Month of oviposition	1,50	0.749	0.757	1,78	0.662	0.419

Dependent Variable	Source of Variation	*C. signifera*			*L. ewingii*		
		d.f.	*F*	*P*	*d.f.*	*F*	*P*
	Logging Treatment	1,50	0.803	0.339	1,78	12.833	0.001
Days to hatching	Month of oviposition	1,50	0.119	0.732	1,78	1.974	0.164
	Logging Treatment	1,50	3.630	0.063	1,78	0.885	0.350
SVL at metamorphosis	Month of oviposition	1,49	8.553	0.005	1,65	1.575	0.214
	Logging Treatment	1,49	0.056	0.814	1,65	0.113	0.738
Mass at metamorphosis	Month of oviposition	1,47	1.280	0.264	1,69	0.186	0.668
	Logging Treatment	1,47	0.090	0.756	1,69	0.870	0.354
Duration of the larval	Month of oviposition	1,47	0.001	0.976	1,70	0.819	0.369
period	Logging Treatment	1,47	0.307	0.582	1,70	0.089	0.767

Table 13. Results from linear regression between life history traits

Regression variables	*C. signifera*				*L. ewingii*			
	d.f.	*F*	*P*	r^2	*d.f.*	*F*	*P*	r^2
Egg size versus hatch size	1,77	55.917	< 0.001	0.421	1,82	36.236	< 0.001	0.306
Egg size versus time to hatching	1,77	0.184	0.669	0.002	1,82	4.224	0.043	0.049
Egg stage versus time to hatching	1,77	1.329	0.253	0.017	1,77	10.160	0.002	0.119
Hatch size versus SVL at	1,49	0.004	0.952	0.000	1,63	0.117	0.733	0.002

Regression variables	*C. signifera*				*L. ewingii*			
	d.f.	*F*	*P*	r^2	*d.f.*	*F*	*P*	r^2
metamorphosis								
Hatch size versus mass at metamorphosis	1,51	0.477	0.493	0.009	1,67	0.031	0.861	0.000
Hatch size versus duration of the larval period	1,51	0.010	0.092	0.008	1,69	0.232	0.632	0.003
Duration of larval period versus SVL at metamorphosis	1,51	3.273	0.076	0.061	1,65	6.175	0.016	0.088
Duration of larval period versus mass at metamorphosis	1,51	4.072	0.049	0.075	1,68	35.821	0.000	0.345

Table 14. Results from Kolmogorov-Smirnov two-sample tests examining the effect of logging treatment and month of oviposition on categorical life history traits

Dependent Variable	Source of Variation	*C. signifera*	*L. ewingii*
		Asymp. Sig. (2 tailed)	
Number hatching per clutch	Month of oviposition	1.000	0.484
	Logging treatment	0.002	0.934
Number metamorphosing per clutch	Month of oviposition	0.999	0.408
	Logging treatment	0.552	0.031

Crinia signifera

Overall mean egg size, calculated for all stages, was 1.72 ± 0.014 mm (n = 87, range = 1.383 – 2.033 mm). The relationship between egg size and stage was highly significant. Eggs laid in September and October (early spring) did not differ significantly in size; however, eggs laid at ponds surrounded by logged forest were significantly smaller than those laid at ponds surrounded by unlogged forest (1.68 ± 0.020 mm and 1.74 ± 0.021 mm, respectively).

Sixty percent of all 270 eggs hatched. These eggs came from 90 clutches, each represented by 3 eggs. All eggs hatched in 58% of clutches, 2 eggs hatched in 23% of clutches, one egg hatched in 13% of clutches and no eggs hatched in 6% of clutches. Significantly more eggs per clutch hatched from logged ponds than from unlogged ponds (91% and 67%, respectively). Month of oviposition did not affect the number of eggs hatching per clutch.

Overall mean hatch size was 3.68 ± 0.032 mm (n = 79, range = 3.16 – 4.46 mm). Egg size was a significant determinant of size at hatching. Despite this, there was no significant difference in hatch size with logging treatment (maybe because reduced sample sizes reduced residual degrees of freedom). Size at hatching was not significantly related to month of oviposition. Egg size, egg stage, logging treatment and month of oviposition did not influence the time to hatching.

Overall, 31% of all eggs collected and 42% of eggs that hatched completed metamorphosis. Logging treatment and month of oviposition did not affect the

proportion of clutches completing metamorphosis. Overall mean SVL at metamorphosis was 9.14 ± 0.075 mm (n = 52, range = 7.40 – 10.60 mm). Initial tadpole size, duration of the larval period and logging treatment were not significant determinants of SVL at metamorphosis; however, the SVL of metamorphs from eggs laid in September was significantly smaller than that from eggs laid in October (2.20 ± 0.008 mm and 2.24 ± 0.011 mm, respectively).

The overall mean mass at metamorphosis was 120 ± 45.0 mg (n = 52, range = 40 – 220 mg). Initial tadpole size was not a predictor of metamorphic mass. Although the relationship between duration of the larval period and mass at metamorphosis was significant, only a small amount of the variance (8%) was explained by the relationship. Logging treatment and month of oviposition did not significantly affect mass at metamorphosis. The overall mean duration of the larval period was 71.0 ± 1.99 days (n = 50, range = 45 - 128 days). Hatch size, logging treatment and month of oviposition were not significantly correlated with the duration of the larval period.

Litoria ewingii

Overall mean egg size (calculated for all stages) was 1.73 ± 0.017 mm (n = 87, range = 1.43 – 2.03 mm). There was a significant relationship between egg size and stage. Eggs laid in September did not differ significantly in size from those laid in October; however, eggs from logged sites were smaller than those from unlogged sites (1.64 ± 0.223 mm and 1.78 ± 0.20 mm, respectively).

Eighty eight percent of all 270 eggs hatched. These eggs came from 90 clutches, each with three eggs. All eggs hatched in 74% of clutches, two eggs hatched in 17% of clutches, one egg hatched in 6% of clutches and no eggs hatched in 3% of clutches. The fraction of eggs hatching from each clutch did not differ between logging treatments and was not influenced by month of oviposition.

Overall mean hatch size was 4.10 ± 0.033 mm (n = 85, range = 3.32 – 4.70 mm). The regression of initial egg size against hatch size was significant. Hatch size was not affected by the month in which eggs were laid; however, the difference in egg size between unlogged and logged sites was carried over to hatch size (4.22 ± 0.054 mm and 3.97 ± 0.047 mm, respectively).

Egg size and egg stage were significant predictors of time to hatching but explained only 5% and 12% of the observed variation, respectively. Logging treatment and month in which eggs were laid did not affect time to hatching. Overall, 44% of all eggs collected and 50% of eggs that hatched completed metamorphosis. The fraction of individuals metamorphosing from each clutch was slightly greater in logged than unlogged sites (54% and 40%, respectively).

Overall mean SVL at metamorphosis was 13.56 ± 0.102 mm (n = 65, range = 10.90 – 15.60 mm). Initial tadpole size did not affect SVL at metamorphosis. The duration of the larval period was a significant determinant of SVL at metamorphosis but only explained 9% of the variation. The effect of logging treatment and month of oviposition on SVL at metamorphosis was not significant.

Overall mean metamorphic mass was 390 ± 7.0 mg (n = 69, range = 240 – 510 mg). There was no significant relationship between initial tadpole size and metamorphic mass; however, duration of the larval period was a significant predictor of metamorphic mass, explaining 35% of the observed variation. Logging treatment and month of oviposition did not significantly affect mass at metamorphosis. The overall mean duration of the larval period was 118.7 ± 2.94 days (n = 70, range = 80 - 225 days). Hatch size, logging treatment and month of oviposition did not significantly affect the duration of the larval period.

DISCUSSION

Our experimental findings indicate that egg size was greater at unlogged than logged sites for both species. Given that genetic effects can be discounted and egg size is unlikely to be related to female size (see Appendix 2), differences in egg size are likely to be a response to environmental heterogeneity associated with logging treatment More specifically, differences in egg size are either due to environmental differences that females are exposed to throughout their development (and hence, differences in phenotype such as body size or condition) and/or they may be due to environmental differences that occur during gamete development itself.

Two possible environmental effects that may explain differences in egg size with logging treatment are variations of food abundance and temperature. Clearing of vegetation has been found to reduce density of invertebrates (Madden *et al.* 1976;

Newman 1991; Van Wilgenburg *et al.* 2001) and to increase temperatures on the forest floor (Raymond and Hardy 1991; Rothermel and Semlitsch 2002; Vanderwoude and de Bryun 2000).

Both lower temperatures and better nutrition during vitellogenesis can increase egg size directly (Berven 1982b; Girish and Saidapur 2000; Jorgensen 1982; Kaplan 1987; Williamson and Bull 1995) and the exposure of a female to these same conditions throughout her own development will increase body size and/or condition (Berven 1982b), thus altering egg size indirectly, through changes to female phenotype (Kaplan and Salthe 1979; Kulkarni and Pancharatna 1996; Semlitsch and Gibbons 1990). However, it must be noted that increased clutch size has also been correlated with increased body size (Cummins 1986) and a trade-off between clutch size and egg size can occur (Cummins 1986; Kaplan and Salthe 1979). We were able to discount clutch size as a factor influencing egg size for *C. signifera* because other research conducted at the same study site showed clutch size is not influenced by logging treatment and there is no trade-off between egg size and clutch size (B. Lauck, unpublished data). For *L. ewingii*, however, clutch size may have influenced differences in egg size with logging treatment.

Temperature regimes may also explain an absence of seasonal difference in egg size. Analysis of average daily temperatures at the study site (Friedman's non-parametric test) showed that although temperatures were statistically higher in October than September (Asymp. Sig = 0.028) the actual difference in temperature was less than 1 °C (mean temperatures for October and September were 8.9 and 9.7 °C, respectively). The small

temperature difference coupled with microhabitat choice by amphibians (Navas 1996) means that exposure to ambient temperatures is unlikely to have significantly influenced egg size. Although Williamson and Bull (1995), correlated egg size with temperatures experienced in the 30 days prior to oviposition in *C. signifera* from South Australia, a much greater range of temperatures (10 °C) occurred over a much longer breeding season than the narrow range we recorded in an early Tasmanian spring.

Although exceptions are numerous, it is a common assumption that offspring fitness increases as a function of individual egg investment through mechanisms such as greater post hatching energetic reserves, increased locomotory ability (hence greater predator avoidance, foraging ability and increased survival), competitive advantage, exploitation of larger prey, reduced susceptibility to size-limited predators, and reduced exposure to high mortality environments because of increased growth or development rates (Bernardo 1996). In view of this, we tested the life history responses to egg size of both species by raising eggs to metamorphosis under constant laboratory conditions.

Our results largely suggest that increased egg size does not necessarily increase the subsequent fitness of larvae and metamorphs. Despite no differences in initial egg size, eggs laid later in the season by *C. signifera* did develop into larger metamorphs, showing that egg quality is, to some degree, independent of egg size in this species. Williamson and Bull (1989) also concluded that egg size was not the sole determinant of tadpole fitness in *C. signifera*. They suggested that more subtle maternal contributions such as the quality of energy store or paternal contributions might also influence fitness. Nager *et al.* (2000), for example, found that the nutrient content of eggs in the Lesser

Black-backed gull, *Larus fuscus*, is likely to be more important in determining egg quality (fledging success) than the size of the egg. For *C. signifera,* the larger size of metamorphs from eggs laid in October than September may be an adaptation to counter increased larval density and competition experienced by offspring laid later in the season (i.e. priority effects). Alternatively, such an adaptation may maximise the fitness of late emerging metamorphs that have a reduced foraging period before winter and a higher desiccation risk at the time of emergence in late summer. For *L. ewingii*, the timing of oviposition did not have consequences for the fitness of life history traits subsequent to the egg stage, as it did for *C. signifera.*

For *L. ewingii*, differences in egg size between logged and unlogged sites did translate to ensuing differences in size at hatching; however, for *C. signifera*, size at hatching was independent of egg size. Evidence for any correlation between larger size at hatching and fitness seems to be species specific and variable. Parichy and Kaplan (1995), for example, showed that *Bombina orientalis* larvae from larger eggs have higher sprint swimming speeds and Travis (1983) found that increased tadpole size reduced susceptibility to predation. The relationship may, however, be complicated by environmental factors during development. Parichy and Kaplan (1992), for example, found that tadpoles from larger eggs were less susceptible to predation than those from smaller eggs when raised in cold water but the reverse was true when the animals were reared in warm water. In our study, species-specific differences in size at hatching may be explained by species-specific responses to predation pressure. In a laboratory experiment, Peterson (1992) demonstrated that *L. ewingii* was more prone to odonate predation than *C. signifera.* Therefore, there may be an adaptive advantage for the

translation of increased egg size into increased hatch size for *L. ewingii*, but not for *C. signifera*.

Any effect of logging treatment on egg size did not translate into an effect on size at metamorphosis and did not influence the duration of the larval period for either species. Evidence for relationships between egg size, hatch size, size at metamorphosis and duration of the larval period in similar studies is mixed. Laugen *et al.* (2002) found that egg size was a significant predictor of size and growth rate until metamorphosis in *Rana temporaria*. The findings of Tejedo and Reques (1992) for *Bufo calamita*, however, reflect those of our study where initial differences in hatch size were lost well before metamorphosis. Large maternal contributions may only be beneficial when resources are limited. In a laboratory experiment, Parichy and Kaplan (1992) showed that hatching size significantly influenced size at metamorphosis and duration of the larval period in low resource, high competition (i.e. low quality) treatments but not in high quality treatments. Had tadpoles in our experiment been raised under resource limited conditions (e.g. with decreased food abundance, increased predation pressure or in competition with conspecifics), initial differences in egg size may have been maintained until metamorphosis. In nature, exposure of tadpoles to such sub-optimal conditions is the norm and, therefore, differences in maternal reproductive investment may be of greater consequence for these fitness traits than indicated in our laboratory experiment.

Initial differences in egg size associated with forest management were correlated with survival for both species. For *C. signifera*, the fraction of eggs that hatched from each clutch was significantly greater in eggs from logged sites, with 91% of eggs/clutch

hatching and only 67% of eggs/clutch from unlogged sites hatching. In other words, larvae that hatched from smaller eggs had increased fitness in terms of survival when compared with larvae from larger eggs. This trend in survival to hatching for *C. signifera*, however, did not carry over to a greater survival at metamorphosis, indicating that additional individuals hatching in clutches from logged ponds may have been weaker. For *L. ewingii*, however, survival to metamorphosis was substantially (15%) greater for clutches from logged sites, despite there being no differences in hatching success between logging treatments. Therefore, metamorphs derived from smaller eggs had increased fitness in terms of survival when compared with metamorphs from larger eggs. This translates to greater recruitment to the adult stage and a real increase in fitness at metamorphosis for *L. ewingii* from logged ponds. Once again, plasticity in the relationship between egg size and survival is likely. Parichy and Kaplan (1992), for example, found that *Bombina orientalis* larvae developing from smaller eggs had greater survival than those from larger eggs when they developed in colder environments. Conversely, when development occurred in warmer environments, larvae developing from smaller eggs had lower survival than those developing from larger eggs (also see Semlitsch and Gibbons 1990).

Because life history responses subsequent to the egg stage exhibit significant plasticity and our study examined life history responses in only one experimental context (i.e. common laboratory conditions), we can draw few definitive conclusions about the effect of logging on fitness of amphibians. Our data do, however, indicate significant environmental heterogeneity as a result of forest harvesting and our discussion has highlighted differences in food abundance and temperature as two likely reasons for

ecological difference. Such differences are likely to be of importance to the lifetime fitness of metamorphs and adults as they will be exposed to the terrestrial environment upon exiting the pond at metamorphosis. For instance, increases in temperatures on the forest floor as a result of logging may conceivably reduce the survival of metamorphs by increasing desiccation risk and restricting foraging and dispersal. Rothermel and Semlitsch (2002), for example, experimentally showed that juvenile spotted salamanders (*Ambystoma maculatum*) and small mouthed salamanders (*A. texanum*) were more susceptible to dehydration in open fields than forest habitats and movement was significantly farther in forests than fields. Because small body size confers greater desiccation risk (due to a greater surface area:volume ratio), emerging metamorphs are likely to be especially susceptible to dehydration.

A lower abundance of litter invertebrates at logged sites may also exacerbate desiccation risk as metamorphs may be required to move greater distances in order to forage. The poorer body condition that results may increase susceptibility to other ecosystem processes such as parasites and disease, thus reducing long term survival. Reduced nutrition may also reduce lifetime reproductive output relating to body size by decreasing growth rate (Claussen and Layne 1983) increasing the time to or reducing body size at sexual maturity and altering fecundity (Jorgensen 1982; Kaplan 1987; Lehman 1978). Further experimental research is clearly required in order to substantiate and isolate such possibilities and such hypotheses provide clear direction for further study.

The fact that land management practices such as logging can significantly alter amphibian life history is a significant finding. Most previous studies investigating the impact of logging on amphibians have done so by assessing population abundance and/or species richness. Life history studies clearly exhibit significant potential as an alternate approach to investigate such ecological questions and may go some way to explaining *why* rather than just *how* logging affects amphibians. Further research incorporating environmental heterogeneity (see Kaplan 1992), temporal aspects of forest regeneration and species with varying tolerance to logging will increase our understanding of both maternal reproductive investment and the consequences of logging for amphibian fitness.

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Chapter 8: Assessing Fluctuating Asymmetry as a Means of Monitoring the Population Health of the Frog *Crinia signifera* in Response to Logging

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ABSTRACT

Fluctuating asymmetry has been proposed as an alternative indicator of environmental stress and population health. However, a notable feature of research examining the relationship between fluctuating asymmetry and fitness is that of inconsistency. To evaluate the efficacy of fluctuating asymmetry as an indicator of environmental stress resulting from logging and the consequences of logging for amphibian population health, I conducted research in two parts using the frog *Crinia signifera* as my model species. The findings of Study 1 indicate a decrease in fluctuating asymmetry (i.e. environmental stress) but also a decrease in body size and body condition (i.e. fitness) as a result of logging. In Study 2 there was no significant relationship between the levels of subtle asymmetry in individuals and the following fitness traits: clutch size, clutch dry mass, average egg dry mass, oviduct dry mass, testes size, age, body size and body condition. Logging, therefore, did not disrupt fluctuating asymmetry in a predictable manner and it was not possible to determine the significance of reduced levels of

fluctuating asymmetry at logged sites. The measurement of fluctuating asymmetry has limitations as a tool with which to monitor environmental change and fitness responses of amphibians to logging.

Keywords: amphibian · developmental instability · environmental stress · fitness · indicator

INTRODUCTION

During the process of growth and development, an organism is exposed to a multitude of stressors. The developmental stability of an organism is its ability to produce an 'ideal' form (Palmer 1994) or to produce a genetically predetermined phenotype (Alford et al. 1999) when exposed to these stressors. Conversely, developmental instability results when stressors interfere with the ability of organisms to correct against them (Alford et al. 1999), and as a consequence, the 'ideal' form is not produced. Very often the 'ideal' form of an organism is not known; however, for bilaterally symmetrical organisms and/or bilaterally symmetrical structures the ideal form, by definition is one of symmetry (Palmer and Strobeck 1986). Such symmetry provides a reference against which deviations from the norm can be compared.

Fluctuating asymmetry is commonly used as an indicator of developmental instability (Palmer 1994). The important underlying assumption of fluctuating asymmetry is that the development of the two sides of a bilaterally symmetrical organism is influenced by *identical* genes (Clarke 1995). Given this, differences in fluctuating asymmetry can be

attributed to differences in extrinsic (environmental) or intrinsic (primarily genetic inbreeding) stress (Palmer 1994).

Positive correlations between environmental stress and levels of fluctuating asymmetry have been documented in the literature (Leary and Allendorf 1989), and consequently, changes in fluctuating asymmetry within a population may provide a sensitive indicator of changes in population health (Alford et al. 1999; Clarke 1995).

It has been suggested, however, that a change in fluctuating asymmetry may not be sufficient to make it a useful bio-indicator of ecosystem health. Fluctuating asymmetry must reflect changes in population fitness rather than changes in stress, otherwise the significance to be placed on that level of stress is debatable (Floate and Fox 2000; Markow 1995). In other words, environmental stress must affect the ability of a population to reproduce and survive (Floate and Fox 2000). Evidence for a relationship between fluctuating asymmetry and fitness, however, has been mixed (Clarke 1998; Markow 1995; Palmer and Strobeck 1986).

Despite this, alternative indicators of amphibian population health are worth investigating as traditional indicators of environmental health such as species richness or population estimates require large amounts of resources, take large amounts of time and are logistically difficult. These limitations apply especially to amphibian populations because abundance at the breeding sites can fluctuate exceedingly over short periods (Berven 1990; Berven and Grudzien 1990; Blaustein et al. 1994; deMaynadier and

Hunter 1995) possibly making traditional indicators relatively insensitive to the sometimes subtle factors leading to population stress and/or decline.

To evaluate the efficacy of fluctuating asymmetry as an indicator of environmental stress and amphibian population health I undertook an investigation examining variations in fluctuating asymmetry in response to logging. Habitat changes as a result of logging have the potential to both increase and decrease the environmental stress to which resident amphibians are exposed by dramatically altering the local habitat. Although the evidence from North America is highly variable, DeMaynadier and Hunter (1995) found that recent logging led to a general decrease in the abundance of amphibians (although species richness was not similarly affected).

I conducted research in two parts. In Study 1, I conducted a study to determine if fluctuating asymmetry differs in *Crinia signifera* captured at logged and unlogged sites and if any differences were correlated with fitness at the population level. In Study 2, I utilised *C. signifera* specimens obtained as bycatch from an existing litter invertebrate study undertaken in the same study area (Bashford et al. 2001) to further evaluate the relationship between subtle asymmetry and indicators of fitness in individuals.

MATERIALS AND METHODS

The Study Organism

Crinia signifera (common brown frog) is a small frog with an adult snout vent length of 20-30 mm (Robinson 1996). The species is found in a wide range of habitats, is common

throughout south-east Australia and is abundant at the study site. In Tasmania, it breeds in both permanent and ephemeral standing water and has its peak breeding season predominantly during spring and early summer (August – January).

The Study Area

The study area was centred on the commercial forests of the WARRA Long Term Ecological Research (LTER) site, Tasmania, Australia (43°3'S; 146°39'E). Vegetation at the site consists predominantly of temperate broad leaf forest (mainly *Eucalyptus obliqua* wet forest). The logging and fire history at the site have resulted in a full range of successional stages of this forest type (www.warra.com). Standard logging practices in wet and mixed forests at the site consist of clearfell, burn and aerial sowing with eucalypt seed on a rotation of 90 years (Hickey and Neyland 2000).

Study 1

I collected frogs from four ponds surrounded by logged and five surrounded by unlogged coupes. Logged sites were defined as those with more than two years but less than five years since logging as the expression of fluctuating asymmetry requires a period of development during exposure to the 'stress' (Clarke 1995) and more recent logging may not have provided sufficient temporal exposure. The choice of recently logged sites also allowed me to discount any effects of adaptation. Unlogged sites were defined as those sites with more than 35 years since logging but four out of the five sites had never been logged. *Crinia signifera* has an extended breeding period and males, in particular, spend significant amounts of time at breeding sites (Lemckert and Shine

1993), thus ensuring extended exposure to the environment in each particular logging treatment.

Ponds were sampled once weekly between 20 September 2001 and 27 October 2001. Flat pieces of wood, obtained from the area surrounding ponds, were placed at the bank/water interface at the edge of each pond. Any frogs found beneath these cover-boards were placed in individually labelled containers with a small amount of water. Because the ventral markings of each frog are unique, digital photographs allowed identification of individuals. Recaptured frogs were not re-measured.

Six metrical traits were measured for each frog: length of forearm, 1st phalange, 2nd phalange, 3rd phalange, femur and tibio-fibula. Three replicate measurements were conducted of each trait, on each side. Palmer (1994) recommended taking replicate measurements of each trait 'blind' (i.e. without reference to previous measurements) to minimise measurer bias. This was achieved by measuring four animals simultaneously and undertaking one round of measurements (all traits and sides of all frogs once) before repeating measurements on all frogs for the second and third replicate measurements. This way, any measurements taken on the first frog had been forgotten after having measured three other frogs. Measurements were taken using a light microscope fitted with an eyepiece micrometer at a magnification of x6.7. Temporal separation of replicate measurements (Palmer 1994) were not undertaken because I anaesthetised animals in order to improve measurement precision and wanted to minimise the exposure of animals to this treatment.

Frogs were anaesthetised before measurements using benzocaine solution (200mL saturated solution of ethy-p aminobenzoate in ethanol diluted to 1 L in water). Kaiser and Green (2001) found the teething ointment Oragel® (with benzocaine as the active ingredient) to be a safe anesthetic for frogs. A shallow layer of benzocaine solution was poured into the bottom of four petri dishes. A frog was placed in each dish and the lid replaced until it was anaesthetised to the point where its limbs could be moved by a researcher with little defensive counter-movement. The frog was then rinsed in distilled water and placed, stomach down, on a piece of glass. Care was taken to minimise the spread of any disease between frogs by covering the glass with plastic wrap before new measurements and sterilising all equipment between measurements. Each frog was positioned to allow the easy measurement of each trait on both sides of its body. Frogs were moistened with drops of water throughout the measuring process to reduce dehydration stress. After each replicate of measurements, each frog was lifted and then replaced on the glass to make sure that the previous position didn't bias measurements. Upon completion of all measurements, frogs were returned to their original field collection container with a small amount of water in the bottom, and allowed to recover (a process that usually took around 30 minutes). All animals were released at their point of capture on subsequent field visits.

In Study 1, body size and body condition were used as fitness indicators and required the measurement of snout vent length and mass of each frog. Body condition was calculated as $mass^{(1/3)} * svl^{-1}$ (pers. comm. R. Alford).

Study 2

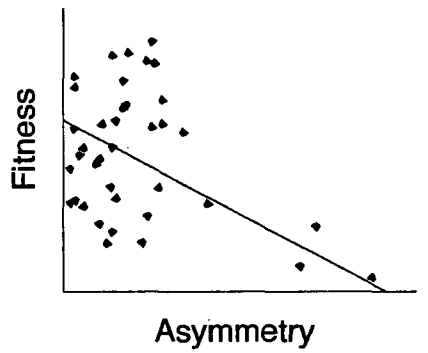
Crinia signifera specimens were obtained as bycatch from an existing lethal pitfall trap litter invertebrate study at the Warra LTER (Bashford et al. 2001). Each specimen was patted dry with paper towelling before mass was measured using an electronic balance (±0. 5 μg) and Snout Vent Length (SVL) was measured using Vernier callipers (±0.05 mm). Specimens were dissected and testes, oviducts, eggs and left and right femur and tibio-fibula were removed for further analysis. To determine dry mass, one oviduct was haphazardly chosen from each individual and dried for approximately 4 weeks at 55 °C to constant mass. Eggs were counted and dry mass determined as for oviducts. The length of both testes was measured. To determine the degree of fluctuating asymmetry, the length of both left and right femur and tibio-fibula were measured for each individual at a magnification of x15 using a binocular microscope fitted with an eyepiece micrometer. Three replicate measurements were made and measurements were taken blind (ie. with intervals of greater than one day between replicates) as recommended by Palmer and Strobeck (1986). Body condition was calculated as in Study 1 (above).

Data Analysis

In both Study 1 and 2, statistical analyses of fluctuating asymmetry was conducted as described by Palmer and Strobeck (1986), Palmer (1994) and Alford et al. (1999). The significance of confounding factors in fluctuating asymmetry analysis (i.e. measurement error, DA, antisymmetry, size) was conducted using a Model III ANOVA with sides (fixed) x individual (random) for each trait (Palmer 1994). Two indices of fluctuating

asymmetry were reported, FA1 and FA10 (Palmer 1994). FA1 ($|R-L|$) is the simplest index and provides a good intuitive understanding of what is happening within the data. It is heavily biased by directional asymmetry and antisymmetry and depends on overall size (Palmer 1994). FA10 is calculated using ANOVA and estimates fluctuating asymmetry after partitioning out measurement error from the overall between-sides variances. This index is not biased by directional asymmetry, or heavily biased by antisymmetry, but is sensitive to overall size. MANOVA was conducted on $|R-L|$ (with logging treatment as the fixed effect and traits as the dependent variables) to determine whether fluctuating asymmetry differed between logging treatments in Study 1. ANOVA was used to analyse differences in fitness traits between logging treatments in Study 1. Due to sexual size dimorphism and because relatively few females were captured, analyses in Study 1 were conducted for males only. Scatter plots were used to determine any relationship between fitness traits and unsigned asymmetry in Study 2. Asymmetry-fitness relations are expected to have a triangular bivariate distributions (Leung and Forbes 1997; pers. comm. Ross Alford) because individuals with high levels of asymmetry are expected to have low fitness whereas individuals with low levels of asymmetry can have both high fitness (because they are developmentally stable) or low fitness (because they developmentally unstable but have low asymmetry by chance) (see Figure 14). Since age, total eggs per clutch, average egg mass, total clutch mass and testes size were significantly correlated with body size (unpublished data), the effect of body size was removed by dividing all fitness traits by SVL in Study 2. Separate analyses were conducted for males and females due to significant sexual size dimorphism.

Figure 14. The expected pattern between unsigned asymmetry (abs(FA1)) and fitness if fitness is negatively related to asymmetry within a population (adapted from Leung, 1997)



RESULTS

Study 1 - Fluctuating Asymmetry

Measurement error as a percentage of non-directional asymmetry can be high (Palmer 1994). The interaction variance term (i.e. sides x individual) indicated that non-directional asymmetry (antisymmetry + fluctuating asymmetry) could be distinguished from measurement error for all traits (Table 15). A significant 'sides' variance term indicates the presence of significant DA and a consequent deviation from 'ideal' fluctuating asymmetry. Significant levels of DA may artificially inflate some indices of fluctuating asymmetry and may indicate the presence of a genetic component of between sides variation (Palmer 1994). Therefore traits exhibiting non-significant levels of DA are preferred. The forearm, 1st phalange and 2nd phalange were found to have insignificant levels of DA; however, DA was significant in the 3rd phalange, femur and tibio-fibula. The levels of DA was removed statistically from the later three traits by subtracting (mean (R-L))/2 from the side with the larger mean and adding it to smaller

side of all individuals in the sample (Palmer 1994). Reanalysis of data verified that DA had been successfully removed (Table 15).

Table 15. Results of ANOVAs testing the confounding factors of fluctuating asymmetry

Trait	Source of Variation	*df*	*F*	*P*
Forearm	Side	1,482	0.453	0.502
	Side x individual	120,482	1.604	<0.001
1st phalange	Side	1,480	0.004	0.948
	Side x individual	119,480	2.691	<0.001
2nd phalange	Side	1,484	0.020	0.920
	Side x individual	120,484	2.570	<0.001
3rd phalange	Side[1]	1,475	23.915	<0.001
	Side[2]	1,475	0.429	0.514
	Side x individual	118,476	2.253	<0.001
Femur	Side[1]	1,484	22.654	<0.001
	Side[2]	1,484	0.110	0.741
	Side x individual	120,484	15.602	<0.001
Tibio-fibula	Side[1]	1,478	10.853	0.001
	Side[2]	1,478	0.471	0.494
	Side x individual	119,478	4.146	<0.001

[1] before statistical adjustment for directional asymmetry

[2] after statistical adjustment for directional asymmetry

Visual inspection of frequency distributions of (R-L) did not indicate skewness, platykurtosis or significant departure from normality for all traits. Kolmogorov-Smirnov tests confirmed these patterns (Table 16). This demonstrates that anti-symmetry (which

may inflate some fluctuating asymmetry indices) is an insignificant component of non-directional asymmetry (i.e. antisymmetry + fluctuating asymmetry) and, therefore, non-directional asymmetry can be used as a valid estimate of the level of fluctuating asymmetry.

Table 16. Levels of directional asymmetry (computed after taking average of replicate measurements as in Palmer (1994))

Sample	Trait	*n*	(R-L)					
			Mean	± SE	Skew	± SE	Kurtosis	± SE
Logged	Forearm	69	0.013	0.009	0.160	0.289	0.569	0.570
	1st phalange	67	0.005	0.013	-0.641	0.293	2.782	0.578
	2nd phalange	68	0.018	0.010	0.386	0.291	-0.400	0.574
	3rd phalange	66	0.004	0.008	-0.289	0.295	0.144	0.582
	Femur	69	-0.018	0.038	0.286	0.289	0.056	0.570
	Tibio-fibula	69	-0.010	0.013	0.045	0.289	0.873	0.570
Control	Forearm	53	-0.005	0.014	0.228	0.327	0.692	0.644
	1st phalange	53	-0.006	0.011	1.137	0.327	3.363	0.644
	2nd phalange	53	-0.016	0.014	-0.038	0.327	0.058	0.644
	3rd phalange	53	-0.015	0.011	-0.883	0.327	1.278	0.644
	Femur	52	0.049	0.059	0.232	0.330	-0.078	0.650
	Tibio-fibula	51	0.031	0.016	-0.521	0.333	1.290	0.656

Trait size may also confound estimates of fluctuating asymmetry. To check for size dependence of fluctuating asymmetry within samples, $|R-L|$ was plotted against an independent measure of body size (snout vent length - SVL) to test for any relationship. Both the plots and the slopes of these regressions (

Table 17) provide no evidence of a size dependent component to fluctuating asymmetry.

Table 17. Dependence of fluctuating asymmetry indices on trait size (computed after taking average of replicate measurements as in Palmer (1994)). Regressions between |R-L| and SVL were used to assess dependence of FA indices on trait size *within* samples and (R+L)/2 was used to assess dependence of FA indices on trait size *among* samples

Sample	Trait	*n*	(R+L)/2		Regression |R-L| vs SVL		Regression Log(var(R-L)) vs mean (R+L)	
			Mean	± SE	Slope	± SE	Slope	± SE
Logged	Forearm	69	3.985	0.063	-0.0028	0.004	-0.1530	0.139
	1st phalange	67	1.498	0.018	0.0015	0.005	0.5000	0.407
	2nd phalange	68	2.515	0.027	0.0013	0.004	0.0694	0.258
	3rd phalange	66	1.441	0.018	0.0020	0.003	0.0775	0.273
	Femur	69	7.099	0.057	0.0021	0.012	0.1080	0.112
	Tibio-fibula	69	7.504	0.060	0.0096	0.005	-0.0559	0.083
Control	Forearm	53	4.086	0.044	0.0032	0.004	0.2420	0.163
	1st phalange	53	1.553	0.024	0.0026	0.003	0.8220	0.318
	2nd phalange	53	2.610	0.028	0.0049	0.003	-0.1070	0.293
	3rd phalange	53	1.501	0.019	0.0064	0.003	0.1590	0.356
	Femur	52	7.275	0.060	-0.0003	0.015	-0.0426	0.162
	Tibio-fibula	51	7.642	0.060	-0.0004	0.004	0.0839	0.086

All traits were found to exhibit ideal fluctuating asymmetry and could, therefore, be used to compare fluctuating asymmetry between logged and control sites.

Replicate measurements of FA1 were used to partition out measurement error in FA10 as in Palmer (1994) (Table 18). Also presented in Table 18 is the measurement error index ME2, a descriptor of measurement error calculated as the square root of the error MS (Palmer and Strobeck 2003).

Table 18. Results for the fluctuating asymmetry indices FA1 and FA10. FA1 was computed after taking average of replicate measurements as in Palmer (1994)

Sample	Trait	*n*	|R-L| = FA1		FA10			
			Mean	± SE	MS_m	σ^2	*df*	ME2
Logged	Forearm	69	0.069	0.006	0.0053	0.00076	6.829	0.0731
	1st phalange	67	0.083	0.009	0.0050	0.00358	34.872	0.0708
	2nd phalange	68	0.077	0.007	0.0048	0.00159	18.901	0.0692
	3rd phalange	66	0.070	0.005	0.0033	0.00121	20.362	0.0573
	Femur	69	0.272	0.020	0.0144	0.04780	63.564	0.1201
	Tibio-fibula	69	0.103	0.008	0.0049	0.00458	41.861	0.0700
Control	Forearm	53	0.092	0.009	0.0081	0.00179	9.299	0.0902
	1st phalange	53	0.071	0.007	0.0052	0.00163	13.929	0.0719
	2nd phalange	53	0.098	0.007	0.0043	0.00381	31.079	0.0657
	3rd phalange	53	0.084	0.006	0.0039	0.00203	21.764	0.0628
	Femur	52	0.353	0.033	0.0152	0.07943	51.261	0.1232
	Tibio-fibula	51	0.106	0.009	0.0041	0.00484	34.714	0.0639

The MANOVA using FA1 showed that fluctuating asymmetry was significantly higher in unlogged than logged sites (Pillai trace = 0.055, $F_{6,685} = 6.649$, $P = <0.001$). This trend was consistent across traits (Table 19).

Table 19. Mean (± SE) of fluctuating asymmetry for each trait for each logging treatment

Trait	Logged		Unlogged	
Forearm	4.046	± 0.014	4.113	± 0.016
Phalange 1	1.504	± 0.009	1.554	± 0.010
Phalange 2	2.521	± 0.011	2.611	± 0.013
Phalange 3	1.448	± 0.008	1.502	± 0.009
Femur	7.115	± 0.025	7.287	± 0.028
Tibio-fibula	7.521	± 0.024	7.640	± 0.027

Table 20. Results of ANOVA testing for differences in fitness traits between logged and unlogged sites

Source of Variation	*df*	*F*	*P*
SVL	1,120	9.742	0.002
Mass	1,120	18.151	<0.001
Body condition	1,120	14.453	<0.001

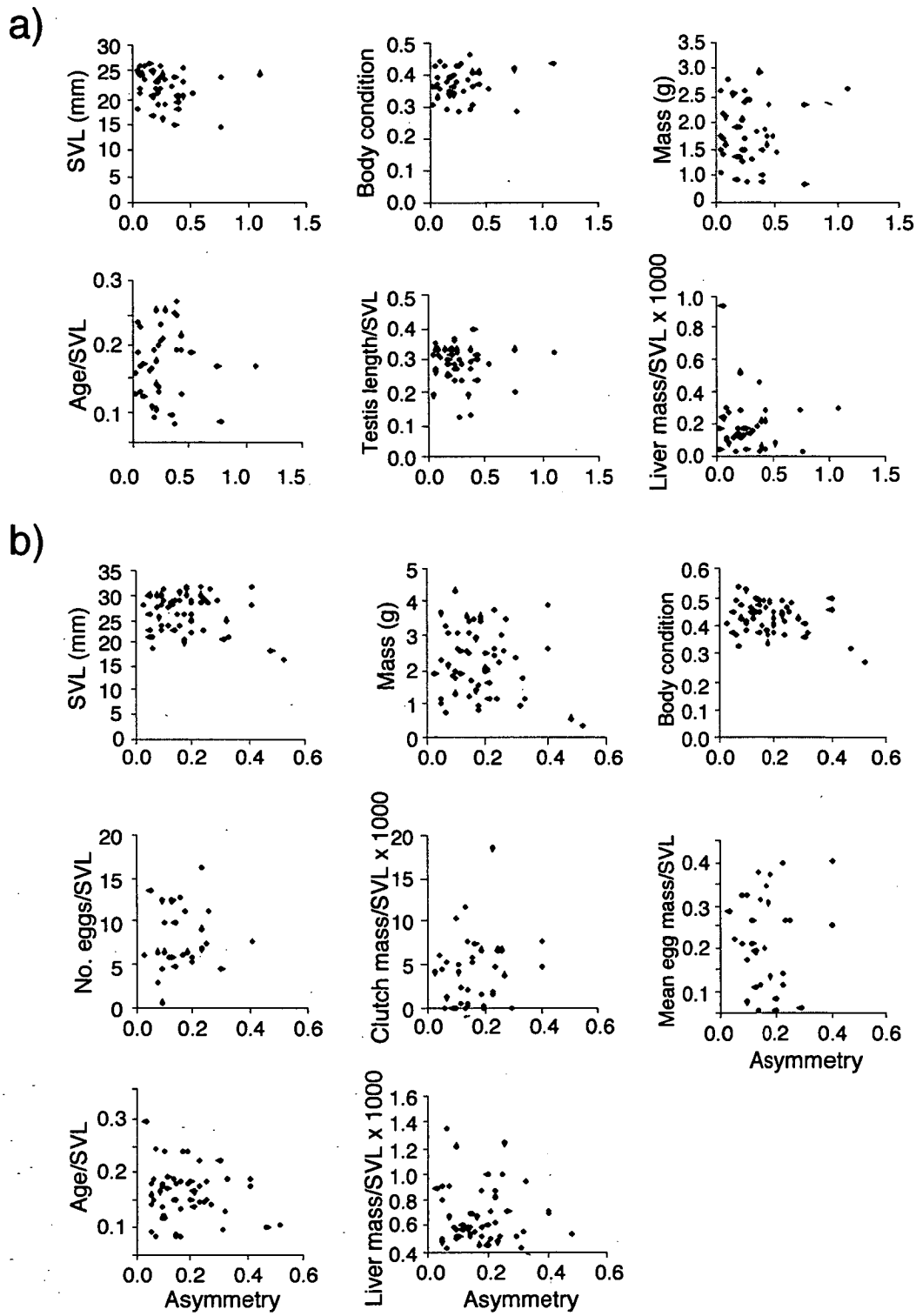
Study 1 - Fitness

Fitness comparisons between logged and unlogged sites are presented in Table 18. Analysis showed that snout vent length was greater at unlogged than logged sites (mean and standard error of 25.9±0.234 mm compared to 25.0±0.210 mm). Mass of males was also significantly greater at unlogged than at logged sites (mean and standard error of 1.54±0.034 g compared to 1.35±0.031 g). Similarly, males at unlogged sites had better body condition than those at logged sites (mean and standard error of 0.39±0.003, compared to 0.376±0.002).

Study 2

No of the relationships between fitness traits and unsigned asymmetry were significant (Figure 15.)

Figure 15. Scatter plots showing the relationship between unsigned asymmetry and fitness traits (a) in males and (b) in females



DISCUSSION

One of the challenges of conservation biology is to identify and measure the ecological effects of land management. This is often achieved by measuring relative population abundance and species richness. Populations of amphibians, however, exhibit high diurnal, seasonal and annual variability, which means that a large amount of research effort and time is required in order to separate natural variations in population fluctuations from those caused by land management (Pechmann and Wilbur 1994).

Developmental instability has been positively correlated with environmental stress (Leary and Allendorf 1989), and has been proposed as an alternative indicator of population health (Alford et al. 1999). Clarke (1995) highlighted a number of advantages that the measurement of developmental instability may have over more traditional monitoring techniques: it is non-specific with respect to the source of environmental stress; it may be more sensitive; it can be measured non-destructively; it is inexpensive; and it is simple to perform.

In this study I investigated the value of measuring fluctuating asymmetry as an approach with which to indicate ecosystem stress and population health of the amphibian *C. signifera* in response to recent logging.

To be of any value as a biomonitor of ecosystem stress, it must be assumed that variations in fluctuating asymmetry have consequences for fitness (Markow 1995) and, in particular, that fluctuating asymmetry is negatively related to fitness; otherwise, the

significance of any variations in fluctuating asymmetry as a result of stress is unknown (Floate and Fox 2000).

However, a notable feature of reviews that have examined the link between relationship between fluctuating asymmetry and fitness (Clarke 1998; Leung and Forbes 1997; Markow 1995; Palmer and Strobeck 1986) is inconsistency. For example, out of fourteen studies adequately investigating the relationship between symmetry and survival re-reviewed by Clarke (1998), one showed no effect, two showed a positive relationship, three were ambivalent and eight demonstrated a negative relationship. Ambivalent studies identified stress, age, sex and life stage as sources of variation. Furthermore, it is likely that studies contradicting theoretical assumptions (i.e. those showing no effect or positive association between fluctuating asymmetry and fitness) are under-represented in the literature merely because they tend not to get published (Markow 1995).

Inconsistencies in the literature may be the result of inconsistencies and inadequacies in experimental methodology and data analysis (Palmer and Strobeck 1986). Reviews have also emphasized a general inadequacy in our understanding of the specific mechanisms affecting both the relationship between fluctuating asymmetry and environmental stress, and fluctuating asymmetry and fitness.

To examine if the measurement of fluctuating asymmetry can be used as a tool for monitoring the effect of logging on the population health of amphibians (using *C. signifera* as a model species), I tested differences in fluctuating asymmetry and fitness

among populations exposed to two logging treatments: recently logged and unlogged (Study 1). Although appropriate for monitoring programs, this population scale can add little understanding to the specific relationships between subtle asymmetry and fitness because there is no way of determining whether developmentally unstable individuals are less fit than stable ones (Clarke 1998). As a result I also examined the specific relationship between fitness and subtle asymmetry in *C. signifera* within a population (Study 2).

In Study 2, increases in fluctuating asymmetry did not have consequences for reproductive output (i.e. size-adjusted average egg mass, total clutch mass, total number of eggs and testes size). Fluctuating asymmetry was also uncorrelated with the indirect measures of fitness of body size (SVL and mass) and body condition (fitness indicators also used in Study 1). Within populations, therefore, less developmentally stable individuals do not exhibit decreased levels of fitness for any trait.

However, comparisons among populations identified lower levels of fluctuating asymmetry at logged habitats (i.e. a decrease in environmental stress associated with logging) and smaller body size and lower body condition in populations from logged habitats (i.e. a decrease in fitness as a result of logging).

By itself, a reduction in stress associated with logging is not entirely surprising as *C. signifera* is not excluded by logging and readily colonises disturbed habitat (a characteristic making it an ideal model species for such an examination). However, given that no relationship was found between fitness traits and subtle asymmetry of

individuals within a population, what do differences between fluctuating asymmetry and fitness associated with logging treatment indicate?

Inconsistencies within and among populations have been noted in relation to fluctuating asymmetry and heterozygosity by Palmer and Strobeck (1986). In this review, several studies indicated concurrent trends showing 1) a lack of concordance between multiple asymmetry traits in individuals within a population, and 2) concordance between multiple asymmetry traits averaged across populations. Alternatively, patterns of developmental stability may have been altered by the preservation of samples in Study 2 (McCoy and Harris 2003).

The negative relationship between fluctuating asymmetry and fitness associated with logging treatment may be a consequence of trait choice. Firstly, the fitness traits used in Study 1 may have been an inadequate indicator of fitness. Floate and Fox (2000) argued that the choice of fitness trait should be based on some direct measure of fitness (i.e. the contribution of the individual to the next generation) unless one or more indirect fitness components provided a reliable substitute. They, for example, used both a direct measure of fitness (percentage pupation) and five indirect measures of fitness (adult size, adult longevity, lifetime fecundity, ovariole number and egg viability) but found that none of the indirect fitness components accurately demonstrated a response to stress. Direct measures of fitness for *C. signifera* such as fecundity or survival were not possible given the small number of females captured and the short time scale of the study (*C. signifera* can live for up to seven years (unpublished data)). Choice of fitness trait, however, was based on a large body of literature showing amphibian adult body

size to be positively correlated with fecundity (Berven 1990; Berven and Gill 1983; Kaplan and Salthe 1979; Semlitsch et al. 1988; Williamson and Bull 1995), and male mating success (Berven 1981; Berven 1990; Howard and Kluge 1985). My own research specifically relating to *C. signifera,* also confirms that body size is positively correlated with the number of eggs per clutch, total clutch mass, average egg mass and testes size (unpublished data).

Despite this, evidence linking body size to fitness relates predominantly to females, whereas the fitness indicators used in Study 1 relate to measurements on males. Exceptions relating specifically to males are also evident in the literature. Mac Nally (1981) found no correlation between male body-size and either the ability to maintain a calling station within a chorus or the duration of reproductive activity for *C. signifera.* Morrison et al. (2001) also demonstrated a decrease in male mating success with increasing male size for *Litoria xanthomera.* Although fitness may not be size dependent in males, reproductive success is likely to be correlated with investment in calling (Mac Nally 1981) as *C. signifera* is an extended breeder. Since calling is energetically costly, energy storage deposits (soma, fat-bodies and liver) are likely to be vital to competitiveness and reproductive success in males. Therefore, body condition may a better indicator of fitness in *C. signifera* males than measures of size alone.

Nevertheless, the fitness traits measured in Study 1, remain an inference of fitness and not a direct measure of it. Body size and condition may, for example, be simply a reflection of increased food abundance at unlogged sites (unpublished data) and may be independent of the stressing agent associated with logging treatment.

Secondly, the negative relationship observed between fluctuating asymmetry and fitness in populations from logged habitats may result because the traits chosen for the assessment of fluctuating asymmetry did not greatly influence fitness. All of the traits used in Study 1 compared the length of limbs (a restriction governed by the limited number of bilateral traits that could be measured on live specimens without harming them). By definition, variations in FA are not large (Markow 1995) and may, therefore, not have affected functionality such as locomotion. As a result, they may be easily compensated for and may have few consequences for fitness; i.e. differences in limb length may be statistically significant but not physiologically limiting.

The relationship between fitness and fluctuating asymmetry is unlikely to be simple (Palmer and Strobeck 1986). In Study 1, for example, the biphasic life history of amphibians is an obvious potential complication. The underlying assumption is that life history traits measured on adults are a reflection of the terrestrial habitat to which they have been exposed. However for amphibians, key periods of development also occur in water during the larval stage and these may be expressed as adult asymmetries. For example, differences in pond shading as a result of logging history may affect growth rates (unpublished data; Skelly *et al.* 2002; Werner and Glennemeier 1999) which, in turn, may affect fluctuating asymmetry (Danzmann *et al.* 1986; McKenzie and O'Farrell 1993). Although Kellner and Alford (2003) found that levels of asymmetry reflect recent growth history in the domestic fowl, *Gallus gallus domesticus,* such patterns may vary with species (or even genetic strain) and environmental stress. In amphibians, differences in size at metamorphosis can be maintained through to adulthood (Halliday

and Verrell 1988); however, the persistence of fluctuating asymmetry through to later life stages is unknown (see McCoy and Harris 2003).

Similarly, it may also be possible that variations in phenotypic traits related to fitness and fluctuating asymmetry are a response to different environmental mechanisms. For example, temperature may influence adult fitness traits independently of stress induced fluctuating asymmetry. Logging may increase forest floor temperatures (Rothermel and Semlitsch 2002) and post-metamorphic amphibians are known to attain larger size as a result of development in colder temperatures (Berven 1982b). As a result the fitness trait of body size and body condition may be a response to differing thermal regimes. Although the range of temperatures experienced by amphibians at logged and unlogged sites may differ, neither may be more stressful than the other because resident amphibians may be able to mediate extreme temperatures through behavioural adaptations such as retreat site or microhabitat use (Navas 1996), and nocturnal or diurnal activity. The fitness trait of body size may, therefore, be independent of environmental stress (i.e. fluctuating asymmetry) but, nevertheless, dependent on logging treatment.

Pond age and population age could also confound the fitness trait of body size. Although age was found not to influence subtle asymmetry within populations, it may influence fluctuating asymmetry among populations. In a commercial forest landscape such as that used in Study 1, many permanent standing water bodies are created in conjunction with the forest harvesting process (DiMauro and Hunter 2002). Therefore, pond age in regenerating forests is often related to the time since logging. If logging is recent (as for

the logged ponds used in this study) colonisation of ponds will also be recent and the age frequency of populations at recently colonised ponds is likely to be biased towards younger age groups since the majority of breeding adults will originate from offspring of the earliest colonizers. Linear regression between pond age and average fluctuating asymmetry did not indicate any relationship (r^2=0.000, $F_{1,9}$=0.000, P=0.997) and allowed me to discount this possibility; however, I include such a consideration in my discussion to indicate complexity of real world conditions that must be accounted for if fluctuating asymmetry were to be incorporated into monitoring programs.

Markow (1995) also highlighted the influence of natural selection on the relationship between fitness and fluctuating asymmetry. If natural selection is in operation, then individuals being measured within fluctuating asymmetry studies may not represent the whole population but rather those that have *survived* exposure to stress. Floate and Fox (2000) hypothesised that if the mortality of the most susceptible individuals (i.e. those with the highest fluctuating asymmetry in the population) increased with increasing levels of environmental stress, then fluctuating asymmetry may not be linearly correlated with environmental stress (and, by inference, with fitness). To test such a relationship, they reasoned that the frequency distributions of highly stressed populations and low stress populations would differ. In their study the frequency distribution of unsigned asymmetry in house flies (*Musca domestica.*) was normal for populations exposed to high levels of stress but deviated significantly from normal for populations exposed to low stress levels. Exploratory frequency distributions of unsigned asymmetry for *C. signifera* populations at logged and unlogged sites did not exhibit a similar pattern, indicating that environmental stress associated with logging

treatment may not be sufficient to cause the mortality of developmentally unstable individuals. Such possibilities will, however, need further consideration if relationships between fluctuating asymmetry and fitness are to be understood and fluctuating asymmetry proposed as a monitoring tool (Floate and Fox 2000).

Clearly, the negative relationship between fluctuating asymmetry and fitness with logging treatment for *C. signifera* does not conform to expected theoretical patterns and fluctuating asymmetry and fitness are not disrupted by logging in a predicable manner. As a result, it is not possible to determine the significance of the reduced levels of fluctuating asymmetry found at logged sites. In my discussion, I have highlighted a number of explanations that require further experimental testing in order to increase our understanding of fluctuating asymmetry, fitness and logging. The inconsistent evidence in the literature and the findings I have presented indicate that, without increased understanding of causality, measurement of fluctuating asymmetry has limitations as a tool with which to monitor environmental change and the fitness responses of amphibians to logging.

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Chapter 9: General Discussion

Commercial management in the southern forests of Tasmania has undoubtedly increased the abundance of standing water in the landscape (Martin and Littlejohn 1982). All medium to large water bodies I sampled in the study area were man-made; i.e. they were constructed adjacent to roads as water supplies for the management of fire by Forestry Tasmania. These ponds provided incidental permanent breeding sites for amphibians at the study site. Commercial forest management has also increased the abundance of small, ephemeral standing water in two main ways. Firstly, the activities of harvest machinery during the process of logging itself often produces soil ruts in which water is unable to drain into the underlying soil (Wronski 1984). I found that such water puddling was twice as common in logged coupes as in unlogged forest; although it must be noted that the amount of this type of standing water *suitable for breeding* did not differ because the volume of water was often too small. Secondly, the construction of roads provides long term increases in standing water along road gutters.

In addition to increasing the overall population abundance, the increase in pond density is likely to alter the population structure of anurans. Pond breeding frogs commonly exist as metapopulations (Skelly 2001). A metapopulation follows a cyclic pattern over time where local extinction of a population at one site (in this case a pond) is followed by recolonisation of the site by dispersing individuals from other populations. When the presence of a species is examined at all sites in the landscape at one instant in time, only a fraction of all suitable sites will support breeding populations. Over time, the presence

or absence of breeding populations at individual sites will be highly dynamic. For frogs, studies have found that the rate of pond colonisation decreases (Marsh *et al.* 1999), and the likelihood of local population extinction at ponds increases (Skelly *et al.* 1999), with distance between ponds.

Because commercial forest management has increased pond density and decreased distances between ponds, extinctions of populations are less likely and colonisation from surrounding ponds more likely. As a result, both *C. signifera* and *L. ewingii* were present at all permanent ponds in all study years.

I also found that *C. signifera* can easily colonise experimentally constructed artificial ponds located up to 500 m from a permanent breeding site within two breeding seasons. Considering that the average and maximum distances between permanent breeding ponds in my study area are 0.8 and 2.4 km, respectively, movement between ponds is likely to be frequent for this species.

My colonization experiment also demonstrated that the rate of movement of C. *signifera* through unlogged forest was almost twice that through logged forest (i.e. artificial ponds in unlogged forests were colonised twice as quickly as those located in logged forest). Because they were colonised faster the total reproductive output of artificial ponds (the total number of clutches laid over the two breeding seasons) in unlogged forest was double that of ponds surrounded by logged coupes. After two seasons, however, the total number of ponds colonised did not differ and, as a result, any difference in total reproductive output after that time is likely to be less significant. Therefore, differences

in the rate of movement through the forest are not likely to be catastrophic for species such as *C. signifera* that can rapidly exploit breeding sites. However, for species such as *L. ewingii* that only colonised a quarter as many ponds as *C. signifera* in the same two breeding seasons, logging treatment may have a significant impact on total reproductive output, especially if the location of suitable breeding sites varies appreciably over time.

My colonisation experiment also showed that *C. signifera* disperses evenly throughout the forest landscape for a distance of at least 500 m around permanent breeding sites. The species is likely to be capable of greater dispersion than this but unfortunately high pond density prohibited me from testing this possibility. It is clear, however, that a significant fraction, if not all, of the forest landscape is utilised as habitat by *C. Signifera* and that the management of forests for similar species should consider the broader forest landscape rather than just the immediate vicinity of breeding sites.

I found that both male size and body condition were greater in unlogged than logged sites. There is evidence to suggest that, in some species, increased male size leads to increased male mating success; however, for *C. signifera* this is unlikely to be the case. Mac Nally (1981), for example, found no correlation between male body size and either the ability to maintain a calling station within a chorus or the duration of reproductive activity for *C. signifera* in Victoria. Body condition is more likely to contribute to male mating success as the species is an extended breeder and the longer individuals spend calling at the breeding site, the greater their chance of attracting a mate. Because significant amounts of energy must be devoted to calling, increased energy storage will

allow males to maximise calling endurance before lost body mass must be restored through foraging.

Increased male size, however, may have indirect advantages because amphibians can lose large amounts of moisture through their skin and are, therefore, physiologically restricted to moist habitats. Larger frogs have a smaller relative surface area that reduces the risk of dehydration. Bellis (1962), for example, found that the average body size of frogs was greater in drier habitats. Because they are likely to have greater mobility during drier times, larger frogs may be able to forage and disperse for longer periods than smaller frogs. The fact that colonisation of artificial experimental ponds was two times faster in unlogged than logged forests may also have been influenced by the larger male size recorded in unlogged forest.

Although specific causes for differences in male body size and condition were not identified, both size and condition are influenced by temperature and nutrition, and these two environmental factors are, in turn, modified by logging. For example, invertebrates were twice as abundant in unlogged than recently logged forests (my unpublished data) and the abundance and quality of food is positively correlated with growth, body size (Claussen and Layne 1983; Lehman 1978) and body condition (Jorgensen 1982). Likewise, lower temperatures during development can increase body size (Berven 1982b) and/or condition (Reading and Clarke 1995) and the removal of the overstorey by timber harvesting has been shown to result in increased insolation and higher temperatures on the forest floor (O'Connell 1987; Raymond and Hardy 1991; Vanderwoude and de Bryun 2000).

Differences in temperature and food abundance associated with logging may also affect investment in offspring by females. Eggs laid at unlogged sites were larger than those from logged sites for both *C. signifera* and *L. ewingii*. Lower temperatures and better nutrition during egg development have both been shown to increase egg size (Berven 1982b; Girish and Saidapur 2000; Jorgensen 1982; Kaplan 1987; Williamson and Bull 1995).

Laying larger eggs is commonly assumed to provide greater fitness through greater post hatching energetic reserves, increased swimming speed, competitive advantage, reduced susceptibility to size-limited predators, and increased growth or development rates (Bernardo 1996). I found that larger eggs did hatch into larger larvae for *L. ewingii* but for *C. signifera* any differences in size at the egg stage were not reflected in size at hatching.

However, a greater proportion of smaller eggs from logged sites survived to hatching for *C. signifera* and to metamorphosis for *L. ewingii*. This indicates that 1) increased egg size does not necessarily confer greater fitness, and 2) factors other than egg size, also influence offspring life history traits (e.g. egg quality or paternal contributions).

Although my results indicate that offspring from logged sites had greater survival at different life stages than those from unlogged sites, research is increasingly showing that egg size and its relationship with subsequent fitness traits is dependent upon the specific environment within which development takes place. Parichy and Kaplan (1992), for

example, found that tadpoles from larger eggs were less susceptible to predation than those from smaller eggs when raised in cold water but the reverse was true when the animals were reared in warm water. Because my egg size experiment tested development in only one environment (*viz* constant laboratory conditions) and environments within forest ponds encapsulate a large range of different conditions, the fitness consequences of variation in egg size for forest management are unknown.

I did, however, make an assessment of how different pond environments might affect fitness independently of initial egg size using *L. ewingi*. In the southern forests of Tasmania, commercial forest management can affect pond environments in two main ways. The first way in which logging may alter tadpole habitat is throught the construction of breeding sites. Breeding sites are predominantly man made, the types of ponds constructed may influence breeding site suitability and, hence, the value of the pond for a particular species. Traditionally, the method used to assess the suitability of a breeding site is to correlate the presence or absence of species in ponds with different habitat characteristics. However, because *L. ewingii* was ubiquitous, it provided an ideal opportunity to investigate how habitat characteristics altered tadpole and metamorph life history. To do this I assumed that greater size at metamorphosis and earlier metamorphosis increased individual fitness (Amezquita and Luddecke 1999; Berven and Gill 1983; Semlitsch *et al.* 1988), and that more metamorphs increased population fitness through an increase in the adult population size (Berven 1990).

I found that larger metamorphs were likely to emerge from younger ponds with less established vegetation surrounding them. This was because reduced shading around

these ponds allowed more solar radiation to enter pond waters thus increasing primary productivity and, consequently, the abundance of tadpole food. Less shaded ponds also gave rise to earlier metamorphosis and this may be an advantage because metamorphs emerge from the pond earlier in the summer before dryer, hotter conditions occur.

Larger tadpoles also emerged from higher elevation ponds, presumably due to their colder water temperatures (Berven *et al.* 1979; Smith-Gill and Berven 1979). The maximum number of tadpoles emerged from higher elevation ponds that were located both in closer proximity to other ponds and had steep pond banks; but, because of my statistical approach, I could not separate the effects of pond bank slope and pond isolation. As a result I could not tell if just one or both characteristics were an important influence on tadpole numbers.

The second way in which logging may alter tadpole habitat is through forest harvesting itself. By removing vegetation around the pond margins, logging may reduce shading and this can alter conditions within the pond. For example, decreased shading may increase solar radiation entering pond waters and this, in turn, may increase primary productivity/ food abundance (Skelly et al., 2002; Werner and Glennemeier, 1999) and water temperatures (Werner and Glennemeier, 1999) for tadpoles. It is well known that tadpoles grow to smaller sizes but develop faster at higher temperatures (Berven, 1982a). However, small and large ponds respond very differently to changes in environmental conditions and, therefore, the effect of shading is likely to differ in both types of pond. For example, because of their small water volumes, less shaded ephemeral ponds may dry out faster (i.e. have a reduced hydroperiod) than shaded ponds

because they have higher evaporation rates. Interestingly, some tadpoles can increase the rate at which they development as a response to decreasing pond volume, thus reducing the length of the tadpole stage. They do this in order to maximize survival before ponds dry out but do so at the expense of their final size at metamorphosis (Crump, 1989).

In larger, permanent ponds, tadpole life history responded predominantly to temperature. Increased shading in permanent ponds resulted in increased size at metamorphosis and reduced survival Ponds with more shading, therefore, increased fitness by producing more individuals and ponds with reduced shading increased fitness by producing larger individuals. Because one trait may be an advantage in some environmental conditions and *vice versa*, a range of different shading conditions around permanent ponds is likely to maximise different fitness traits at different times.

In smaller ephemeral ponds, hydroperiod was the predominant influence with tadpoles developing faster in unshaded than shaded ponds. However, had temperatures during that summer been hotter, these ponds may have completely dried before metamorphosis could be completed, thus reducing survival. In such conditions, increased shading around ponds may reduce pond evaporation and enable the completion of metamorphosis. Therefore, varying shading conditions around ephemeral sites may also allow a compromise between tadpoles developing faster and the risk of premature pond drying.

So what does this tell us about how to manage shading around ponds? For a habitat generalist such as *L. ewingii*, a diversity of shading conditions may allow populations to

'hedge their bets' and maximise different fitness traits at different times. Standard forestry practices in which breeding sites used by amphibians are managed for other purposes and provide only incidentally habitat for amphibians, seem to provide the optimal conditions for maximising the fitness of the *L. ewingii* tadpole life stage by providing just such a heterogeneous mix of breeding sites.

CONCLUSIONS

Commercial forest management has lead to an increase in the abundance of breeding sites for *C. signifera* and *L. ewingii* at the study site. Because they are not excluded by logging and are not of any present conservation concern, *C. signifera* and *L. ewingii* were ideal model species for assessing an experimental approach for measuring the impact of logging on amphibians. Such research is timely since forest management invokes considerable public debate and current research relating to amphibians has large knowledge gaps (particularly outside North America).

I have found that logging can significantly influence the life history of anurans at all three stages of their life cycle. Life history studies have proved to be a successful approach to investigating how frogs relate to the forest landscape in Tasmania's southern forests and how they were affected by logging. Although the specific results relating to my two study species are in no way intended to apply to other species with different habitat requirements further use and development of this experimental approach to other situations would increase our understanding of how and why frogs respond to forest harvesting the way they do.

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Appendix 2: Life History of the frog *Crinia signifera* in Tasmania, Australia

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ABSTRACT

I investigated the importance of body size (SVL), age, body condition (males only), season and growth history as determinants of the life history fitness traits in the frog *C. signifera*. Females lived longer and attained a larger size than males by delaying sexual maturity. Most females and males attained sexual maturity after three and two years, respectively. Body size (but not age) was the primary determinant of fecundity, total reproductive output (clutch mass) and oviduct mass for females. Season was the predominant influence on egg size with smaller eggs produced in summer than in other seasons. Direct investment in male gonads (testes size) was determined by body size and also by age. This, and fact that female amphibians are commonly larger than males, suggests that male size is not necessarily the primary determinant of reproductive success in *C. signifera*. In evolutionary history, selection on reproductive traits in females is likely to have acted predominantly on body size, whereas selection in males is also likely to have acted on survival.

INTRODUCTION

Life history theory is based on the assumption that organisms aim to maximise fitness within their lifetime. At a most basic level, the primary goal of any organism is to reproduce (Roff 1992) and maximum fitness is achieved when that organism produces the greatest number of successful offspring within its lifetime (Bell 1980). Lifetime reproductive success, however, is limited by the physiology of the organism and by the resources that are available in a given ecological setting.

A large body of literature has shown that increased body size in amphibians confers significant fitness advantage. For example, body size is positively correlated with fecundity (Kaplan and Salthe 1979; Ponsero and Joly 1998), male mating success (Berven 1981; Howard 1980), mobility within a landscape (Ponsero and Joly 1998), and negatively correlated with desiccation risk (Bellis 1962) and size limited predation.

Growth history is an important determinant of adult body size and thus fitness. Size at metamorphosis, for instance, is often used as an important indicator of overall amphibian fitness because it is often correlated with adult size (Amezquita and Luddecke 1999; Berven 1990), and, therefore, has important repercussions for survival (Berven 1990; Goater 1994), body size at first reproduction (Amezquita and Luddecke 1999; Semlitsch *et al.* 1988) and age at first reproduction (Berven 1990; Semlitsch *et al.* 1988; Smith 1987).

However, age and body condition often co-vary with body size and have also been positively correlated with life history traits influencing fitness (Halliday and Tejedo 1994; Jorgensen 1982; Kulkarni and Pancharatna 1996; Pancharatna *et al.* 2000).

An understanding of how body size, age and body condition regulate the expression of fitness traits allows us to differentiate selective pressures regulating life history adaptations, reproductive output and the fitness of species. For example, in species where growth continues after sexual maturity, individuals gain size and fitness advantage by living longer; however, if growth ceases after sexual maturity then any size advantage is attained by maximising juvenile growth rates (Halliday and Verrell 1988; Marvin 2001).

In this study I investigated some life history traits for *C. signifera* in Tasmania in order to identify the contributions body size, age and body condition have on the regulation of male and female fitness traits. I also investigated age specific growth characteristics and their consequences for life history traits in order to determine the adaptive pressures that regulate selection in this frog.

Materials and Methods

Crinia signifera is widely distributed throughout Tasmania and south-eastern mainland Australia. The species is found in a wide range of habitats (Robinson 1996) and has a flexible life history. It breeds in both permanent and ephemeral sites and in Tasmania breeding is limited to lentic systems. Breeding in the Southern forests of Tasmania occurs predominantly in early spring to mid summer and any autumn breeding seems dependent

on rainfall (pers. obs.). The frog has an adult SVL range of 20-30 mm. Metamorphosis occurs predominantly in January and February.

The study area was located at the Warra Long Term Ecological Research (LTER) site. The Warra LTER is located within the Southern Forests of Tasmania, approximately 60 km south of Hobart (43°3'S; 146°39'E) and has an elevation range of 37-1260 m (Brown *et al.* 2001). The specific aims of the Warra LTER centre on developing an understanding of ecological processes in Tasmania's wet *Eucalyptus obliqua* forests and the demonstration and development of sustainable forest management practices (Warra LTER pamphlet).

Standard logging practices in wet and mixed sclerophyll forests consist of clearfelling, burning and aerial sowing with eucalypt seed (CBS) on a rotation of 90 years (Hickey and Neyland 2000). Trials have also been established at the site to investigate alternative silvicultural practices. To this date, pre-logging and the first phase of post-logging invertebrate sampling have been completed in five coupes. The logging trials included 10% dispersed retention (two coupes), CBS ± understorey islands (two coupes) and a control. For further details regarding these silvicultural treatments see Hickey *et al.* (2001).

One investigative sub-component of these silvicultural trials is to measure the response of invertebrates to alternative silvicultural practices (see Bashford *et al.* 2001). The *Crinia*

signifera specimens I used in my study were obtained as a result of by-catch from wet pitfall traps used in this invertebrate study.

Sampling sites were located within each coupe. Each site consisted of a 50 m transect having 10 pitfall traps. Pitfall traps were arranged in pairs each separated by 1-2 m. Pitfall traps were charged with 100 mL of either 33% ethylene glycol (Castrol RadiCool®) or undiluted ethylene glycol (Castrol). For further detail regarding pitfall trap construction refer to Bashford *et al.* (2001).

Coupes were sampled for as long as logistically possible in the pre-logging phase. Post-logging sampling commenced as soon as feasible after burning and continued for a period of 12 months. Pitfall traps were continuously open during both the pre and post-logging periods and sampling was undertaken at monthly intervals.

Crinia signifera specimens were stored in 70% ethanol after field collection. Each specimen was patted dry with paper toweling before mass was measured using an electronic balance (± 0.005 mg) and snout vent length (SVL) was measured using calipers (± 0.05 mm). Specimens were dissected to remove testes, oviducts, egg clutch, liver, right femur and stomach contents for further analysis. The length and width of both testes was measured using a binocular microscope fitted with an eyepiece micrometer. Eggs in each clutch were counted. Dry mass of livers, stomach contents, egg clutches, and one randomly chosen oviduct from each individual was determined by drying organs for approximately 4 weeks at 55 °C (i.e. to constant mass). Average egg dry mass was

determined by dividing total clutch dry mass by the number of eggs in the clutch. Body condition was calculated as $mass^{(1/3)} * svl^{-1}$ (pers. comm. R. Alford).

The right femur was used to determine the age of each specimen using skeletochronology (Smirina 1994). Femurs were decalcified in 5% nitric acid for 24 hours, then washed overnight in water. They were then embedded in paraffin wax and 7μm sections of the central zone of the diaphysis were cut using a microtome. Sections were stained with Ehrlich's haematoxylin. Lines of arrested growth (LAGs) were counted and 2 perpendicular diameters of the endosteal bone and each LAG were measured using a binocular microscope fitted with an eyepiece micrometer. To test for LAG resorption the average diameter of the first LAG in one-year-old frogs was calculated. Significant bone resorption was considered to have taken place if the average diameter of the resorption line was greater than the mean diameter of the first lag (Hemelaar 1985). An age class of 0.5 was assigned to very small frogs having no identifiable LAGs.

Statistical analysis was undertaken using SPSS™ 10.0. α was set at 0.05. Due to sexual size dimorphism, analyses were conducted separately for males and females. Because of the extremely low capture rates (0.9 individuals/1000 trap days), samples were pooled across years and sites within coupes.

I modelled growth using the relationships between age and body size to fit a von Bertalanffy growth curve (Hota 1994). The general form of the equation is:

$$SVL_t = a(1\text{-}be^{-kt})$$

where, SVL_t = body size at time t, a = asymptotic body size, b = parameter related to initial body size and k = the characteristic growth rate. The parameters a, b and k were estimated using non-linear regression. Sex could not be determined for most specimens in the 0.5 year age class. Data from this age class were randomly attributed to either males or females on the assumption that differences of size at metamorphosis with sex were small and would, therefore, not significantly influence other parameter estimates in the model. This assumption was tested by comparing the coefficient of variation of juveniles in the lowest age class (0.5 years) with subsequent age classes.

I was unable to verify skeletochronological data using mark/recapture methods because my ethics permit did not allow the toe clipping of animals. Skeletochronology has been classed as a routine method of determining age in amphibians (Smirina 1994). There is substantial evidence verifying the technique for temperate (for example, Bruce *et al.* 2002; Castanet and Smirina 1990; Driscoll 1999; Esteban and Sanchiz 2000; Hemelaar 1985; Hota 1994; Smirina 1994) and tropical amphibians with exposure to less seasonal variation (Kumbar and Pancharatna 2001; Morrison *et al.* 2004; Pancharatna *et al.* 2000). The temperate climate in Tasmania and the variable seasonal activity patterns of *C. signifera* (unpublished data) maximise the likelihood that LAGs represent annual variations in growth rates.

I used sequential multiple regression to determine the importance of the independent variables body size (SVL), age, body condition (males only) and season as determinants of the following life history traits: the number of eggs per clutch, total clutch mass, average egg mass, oviduct mass, testes size, stomach mass and liver mass. Unfortunately, low sample numbers in pre-logging and control treatments did not allow me to also assess the effect of silvicultural practices on life history traits. As a result, data from all silvicultural treatments (both pre and post-logging samples) were pooled. Body condition could not be calculated for females because total clutch mass was measured as dry mass and body mass was measured as a wet mass. The independent variables were sequentially entered into the model in the order listed above following the theoretical considerations discussed in the Introduction. Independent variables were included in the model if their unique contribution (i.e. that not already accounted for by the other independent variables previously entered into the model) was significant (i.e. significant part or semi partial correlation). I included the categorical variable 'season' (summer, autumn, winter, spring) in the model by making three indicator variables (with the fourth season as the reference variable) and entering all three indicator variables simultaneously into the model. Stomach contents analyses were only undertaken for females without eggs because eggs in the body cavity may have physically limited the amount of food consumed.

RESULTS

Skeletochronology

LAGs were evident in bone cross sections as concentric, denser lines around the marrow cavity. Those laid down later in life were closer together than those early in life. Age could not accurately be determined in 25 of 179 cross sections because LAGs were unclear. Bone resorption associated with endosteal surface remodeling was evident in 15% of bone cross sections (i.e. 1 lag = 5%, 2 lags = 8%, 3 lags = 2%). Final age in these individuals was adjusted appropriately.

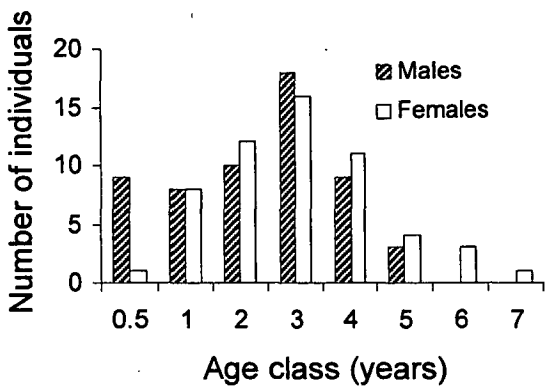
Sex and Age Structure

Fifty-two males and 71 females were sampled. There were 65 juveniles under the age of one year (28 for which sex could not be determined).

Frequency distributions of age for males and females are presented in Figure 19. ANOVA showed that the average age of males was lower than for females (mean ± SE of 2.4 ± 0.18 and 3.0 ± 0.20 years, respectively; $F_{1,112} = 5.388$, $P = 0.022$). The lower average age of males may have been influenced by the higher frequency of individuals in the 0.5 year age class. This was likely to be an artifact of methodology rather than the species' life history. Sexual development in females is slower than males (see below) and it is likely that a large proportion of juveniles for which I could not confirm sex, were immature females having, as yet, no identifiable sex organs. Reanalysis excluding the 0.5

year age class showed no significant difference in the average age of males and females ($F_{1,102} = 1.354$, $P = 0.247$).

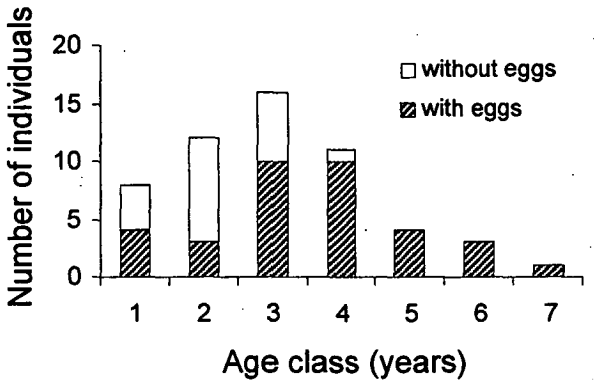
Figure 19. Frequency distribution of age for males and females



On average females can live longer than males: the maximum age of males and females caught was 5 and 7 years, respectively. There were a greater frequency of individuals in the lower age classes of both sexes and a dramatic decrease in frequency of age classes greater than 5 years (only 4.5% of males and 11.2% of females were older than 5 years). Although females can live longer than males, only a very small fraction of the female population actually does so.

The age frequency distribution of vitellogenic females (Figure 20) showed that the minimum age at which eggs were present was 1 year (although very few females under the age of three were vitellogenic). The majority of breeding females were 3 or 4 years old. The proportion of the female population not carrying eggs decreased with age.

Figure 20. Frequency distribution of age for females with and without eggs



Growth

SVL varied substantially in all age classes indicating that the largest individuals were not necessarily the oldest (Figure 21). Initial growth rate was high for both sexes but then slowed with age. The coefficient of variation in SVL increased with age for both males and females (Table 21); likewise that for juveniles in the 0.5 year age class was low (4.18) relative to later age classes. This small coefficient of variation in juveniles justified my assumption that any sexual size dimorphism at this age was small and, therefore, would have a negligible effect on other model parameters. The von Bertalanffy growth model explained 60% and 72% of variation in body size with age for males and females, respectively. The model (Table 22) showed that asymptotic size was greater for females than males (i.e. there was significant sexual size dimorphism). Initial size and characteristic growth rate did not differ with sex. Growth rate decreased significantly after two years and three years of age for males and females, respectively.

Figure 21. von Bertalanffy growth model fitted to size and age data for males and females

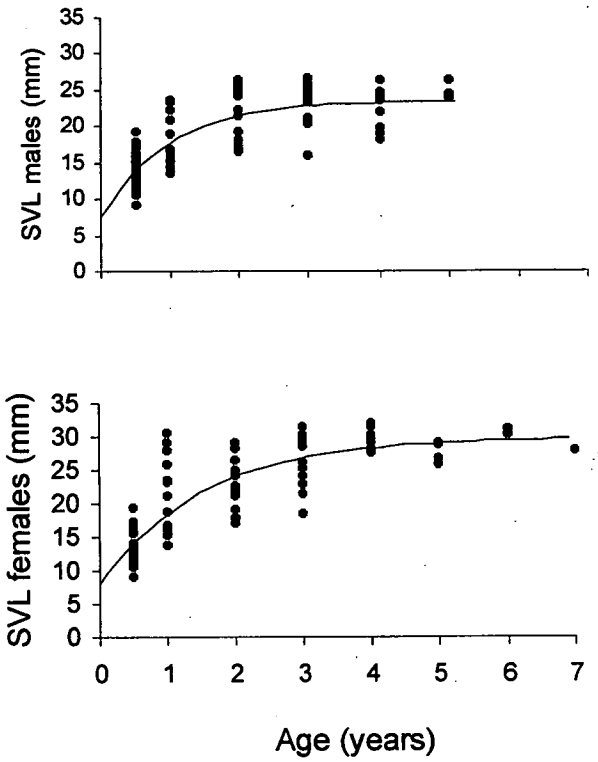


Table 21. Coefficient of Variation (CV) of SVL with age for females and males

AGE	CV for Females	CV for Males
0.5	*	3.36
1	6.14	5.61
2	8.19	6.12
3	6.93	8.40
4	21.62	7.45
5	18.07	19.84
6	56.05	*

* no samples available for age group

Table 22. Parameter estimates for von Bertalanffy growth models for males and females with upper and lower 95% confidence intervals

Sex	a			b			k		
	lower	mean	upper	lower	mean	upper	lower	mean	upper
Male	21.58	23.46	25.34	0.47	0.68	0.89	0.37	1.04	1.71
Female	27.06	29.83	32.59	0.62	0.74	0.85	0.35	0.66	0.97

Multiple regressions between life history traits

The results of multiple regression analysis involving morphological traits can be found in Table 23. The number of eggs, clutch mass, and oviduct mass all increased with female body size and was lower/smaller in summer than in other seasons. Average egg mass was lower in summer than in other seasons. Testes length and male liver mass increased with body size and age. The mass of stomach contents increased with male body size. There was no significant predictor for the mass stomach contents for females.

Table 23. Results of multiple regression between morphological traits

Parameters	Explanatory Variables	R^2	*d.f.*	*F*	*P*
Number of eggs/clutch*	SVL, season	0.420	4,32	5.062	0.003
Total Clutch mass*	SVL, season	0.400	4,41	6.158	0.001
Average Egg mass*	season	0.355	3,32	5.310	0.005
Oviduct mass*	SVL, season	0.417	4,48	7.872	< 0.001
Testes length	SVL, age	0.752	2,54	78.69	< 0.001

Parameters	Explanatory Variables	R^2	*d.f.*	*F*	*P*
Stomach mass (male)	SVL	0.108	1,56	6.651	0.013
Stomach mass (female)#*	-	-	-	-	-
Liver mass (male)	SVL, age	0.412	2,51	13.171	< 0.001
Liver mass (female)*	SVL, age	0.206	2,54	6.757	0.002

* body condition not included as an independent variable in analysis for females (see Methodology)

only for those females without eggs because clutches reduced space in the body cavity and may have influenced the amount of food in stomach

To examine the relationships between egg size, number of eggs and clutch mass, the effect of female body size was removed (by dividing by SVL to obtain *relative* values). There was a positive relationship between relative egg size and relative number of eggs ($r^2 = 0.285$, $F_{1,32} = 12.346$, $P = 0.001$). Relative clutch mass increased with body size ($r^2 = 0.159$, $F_{1,41} = 7.535$, $P = 0.009$).

DISCUSSION

The age structure of *C. signifera* did not differ between males and females despite the fact that the maximum age reached by females was greater than males (seven versus five years, respectively). That males are generally younger than females has been reported in various anuran species (see references in Konsue *et al.* 2001) because males attain sexual maturity earlier and females live longer (Smirina 1994). My findings may be a reflection of the sampling strategy. Because sampling was not conducted solely around breeding sites it is likely to more reflect the overall age structures of the population than just the active breeding component.

In general very few males or females survived past the age of four years and despite the fact that females can live longer than males, only a small fraction actually do so. Differences in longevity associated with sex may be due to sexual size dimorphism; for example, larger female body size may reduce risk of desiccation and size limited predation. Males also mature earlier than females (see below) thus exposing them to increased mortality associated with breeding: extended calling by males at breeding sites may make them more obvious targets to predators than silent females (Lemckert and Shine 1993) and may use up energy reserves that would otherwise be used to maximise survival. Reduced male relative to female survival has also been demonstrated for *C. signifera* by Lemckert and Shine (1993) and Williamson and Bull (1996).

Growth of post metamorphic *C. signifera* exhibited a positive, curvilinear relationship between body size and age with rapid post-metamorphic growth that slowed with age. However, this relationship was weak due to large variance in body size within a given age class. As a result, the relationship is not sufficiently precise to enable accurate determination of age from body size; a pattern that is typical of other amphibians (Halliday and Verrell 1988; Khonsue *et al.* 2001).

Since the magnitude of variation within age classes for *Triturus vulgaris* tended to remain constant, Halliday and Verrell (1988) suggested that initial differences in size early in life (i.e. at metamorphosis) are maintained throughout the lifetime of the individual. Such maintenance of size advantage at metamorphosis through to adulthood has often been

noted for amphibians (Amezquita and Luddecke 1999; Berven 1990; Smith 1987) thus making size at metamorphosis an important trait for the determination of subsequent fitness. However, in my study variation in body size increased with age suggesting that growth history and adult body size are also significantly influenced by terrestrial environmental heterogeneity and perhaps behavioural/genetic differences within post metamorphic individuals.

Females attained a larger asymptotic size than males despite there being no difference in the characteristic growth rates. Such female biased sexual size dimorphism is common in amphibians (Shine 1979).

But sexual size dimorphism cannot be investigated in isolation from sexual maturation, since both may be interdependent. Growth rates in amphibians often decrease at the onset of sexual maturity when resources are allocated to sexual reproduction rather than somatic growth (Halliday and Verrell 1988; Konsue *et al.* 2001; Smirina 1994). Delayed sexual maturity of females relative to males is one strategy used by amphibians that allows females to divert energy to somatic growth over a longer period of time (Bruce *et al.* 2002). In this way, it is possible for females to attain greater body size than males.

For *C. signifera*, this reduction in growth rate (and thus inferred sexual maturity) occurred at two years of age for males and three years of age for females. The minimum age at which eggs were present was one year of age, in agreement with the findings of Williamson and Bull (1996) who also found that *C. signifera* could attain sexual maturity

late in the breeding season following metamorphosis. Williamson and Bull (1996) also reported that most individuals (irrespective of sex) were adults in their second year but some animals had still not have reached maturity approximately two years after metamorphosis. The majority of females with eggs in my study were three or four years old confirming three years to be the age at which the majority of females attained sexual maturity in southern Tasmania.

The fact that amphibian females are commonly larger than males suggests that selection pressures differ for each sex and selection for greater size has more significant fitness advantages for females than males (Halliday and Tejedo 1994). For females, increases in body size relate strongly to increases in fecundity both for other amphibian species (Berven 1982b; Ponsero and Joly 1998) and for *C. signifera* at other sites (Humphries 1979; Lemckert and Shine 1993; Williamson and Bull 1995). For *C. signifera* in my study, body size (and not age) was the most important determinant of fecundity, total reproductive output (clutch mass) and oviduct mass. Larger females also contributed a relatively higher proportion of resources to reproductive output by increasing relative clutch mass. This finding differs from those of Williamson and Bull (1995) and Humphries (1979) who found that larger female *C. signifera* did not contribute a higher proportion of their body mass to reproduction. Larger females also laid both more and larger eggs and, therefore, there was no tradeoff between fecundity and per offspring provisioning.

Larger female body size may also confer increased reproductive success though the laying of multiple clutches within a season. Lemckert and Shine (1993), for example, found larger *C. signifera* females tended to lay multiple clutches. In their study, twenty-nine of forty-nine females produced one clutch, sixteen females produced two clutches, three females produced three clutches and one female was captured in a gravid state having already produced three clutches within a twelve month period. For *Rana catesbeianan*, second clutches had smaller egg diameters and lower clutch mass than first clutches (Howard 1983) indicating that females have a reduced capacity to provision later clutches. Although I could not differentiate between first and consecutive clutches, both clutch size and the number of eggs per clutch were lower in summer than the main breeding season in spring; since few large females appear to miss the opportunity to participate in the spring breeding period, this suggests that these may have been the second clutch for the season.

For *C. signifera* the number of clutches laid per season is likely to be dependent upon the length of the breeding season. The population studied by Lemckert and Shine (1993) south of Sydney was able to breed continuously throughout the year and lay up to four clutches per annum. Humphries (1979), on the other hand, found that female *C. signifera* in Canberra produced up to two clutches in a more restricted six month breeding season. During the three years in which I studied *C. signifera* in Tasmania, a secondary breeding season outside the peak breeding season in August - November occurred only once during the autumn of 2002. This was a particularly wet year indicating that multiple

breeding per season may be rainfall dependent and that overall breeding patterns are likely to be similar to the population studied by Humphries (1979).

Because increased investment in reproduction can come at a cost to survival (Lemckert and Shine 1993), amphibians may also skip breeding in some seasons and this trade-off is seen as a compromise between losing an opportunity to breed and future benefit in fecundity resulting from greater growth rates, energy storage and survival. The proportion of non-vitellogenic *C. signifera* decreased with age and body size, suggesting that delaying reproduction in order to achieve greater body size is likely to be more valuable in early life when growth rates are higher than later when the overall gain in growth is negligible.

Although variation in egg size is also often related to female size (Halliday and Tejedo 1994) the relationship in generally weaker than that between female size and clutch size, suggesting that environmental factors are more influential (see citations in Cummins 1986; Halliday and Tejedo 1994). My findings suggests that seasonal differences in environmental conditions were the predominant influence on egg size with smaller eggs in summer than in other seasons. Once again, this may be because these clutches are the second for the season, and hence, not as well provisioned; however, differences in egg size may also be due to seasonal variation in temperature or nutritional (Berven 1982b; Girish and Saidapur 2000; Jorgensen 1982; Kaplan 1987; Williamson and Bull 1995).

In comparison to females, males invest limited resources in gonads and gametes (Mac Nally 1981) and, as a result, gamete production does not incur a large, direct physiological cost. Male competition, on the other hand, can take many forms (see Halliday and Tejedo 1994) and can ultimately mean that the total reproductive costs of males and females are comparable .

The fact that sexual size dimorphism in amphibians is commonly female biased suggests that male size is not necessarily a determinant of reproductive success. Of the 32 different species reviewed by Halliday and Tejedo (1994), for instance, only 6 demonstrated consistent positive associations between male body size and mating success. Mac Nally (1981) found no correlation between body-size and the ability to maintain a calling station within a chorus, or between body-size and the duration of reproductive activity for *C. signifera* in Victoria. Lemckert (unpublished data) also found not relationship between body size and male mating success for *C. signifera* in New South Wales.

For extended breeders, such as *C. signifera*, male mating success may be positively correlated with attendance at the breeding site and competition between males may take the form of endurance rivalry (Halliday and Tejedo 1994). Therefore, the longer a male remains a resident at the breeding site, the greater reproductive success he may be expected to attain as this maximises the chance of encountering females who only visit breeding site for short periods of time (Lemckert and Shine 1993; Mac Nally 1983). Males that accumulate the most energy are likely to be able to sustain calling the longest without having to supplement energy storage by feeding.

Seasonal variation in body condition is, therefore, expected because calling is metabolically expensive (Mac Nally 1981) and opportunities for feeding may be more limited during the calling period. Unlike *C. signifera* in Victoria (Mac Nally 1983), however, seasonal variation in body condition was not evident in male *C. signifera* in Tasmania. This may be because trapping in my study was not centred on breeding sites and consequently is likely to have included the non-breeding portion of the population that may have greater continuous foraging opportunities. It is also possible that the abundance of food was more consistent from season to season or that a reduced calling period in Tasmania allowed males greater opportunities to forage throughout the year.

It is interesting to note that direct investment in male gonads (testes size) for *C. signifera* in Tasmania was determined also by age. Age was also an important determinant of liver mass in both males and females showing that older individuals can store greater energy reserves. Whereas female selection is likely to act predominantly on growth rates (particularly in early life) (Halliday and Verrell 1988) and adaptations to seasonal conditions, male selection is also likely to act on survival, as older males are likely to be able to sustain calling for longer periods of time due to greater energy reserves and may have greater spermatogenesis and steroidogenic potency of testis due to greater testicular size (Pancharatna *et al.* 2000).

It is evident, therefore, that the process of adaptation in historical evolution is a complex process regulated by many of selective pressures simultaneously acting upon many life history traits. The factors dictating adaptation not only differ between species but also

differ between sexes within the same species. Due to their differing reproductive strategies, *C. signifera* males and females exhibit different life history traits in order to maximise reproductive success. Although morphological differences, such as body size, are significant predictors of reproductive output, other factors such as age and adaptations to season also add to the understanding we have of natural and sexual selection.

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Appendix 3: Seasonal Activity Patterns of the Frog, *Crinia signifera*, in the Commercial Forests of Southern Tasmania, Australia

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ABSTRACT

I investigated the seasonal activity patterns of the frog *Crinia signifera* in commercial forests of Tasmania, Australia subjected to four different silvicultural practices (standard logging practices at the site (clearfell/burn/sow); understorey islands; 10% dispersed overstorey retention; and an unlogged control). Pre and post-logging sampling was undertaken over a period of six years using pitfall traps. Capture data indicated that frogs were most active during summer and least active during winter. Males were caught more frequently than females in autumn and females were more active than males in winter. In the pre-logging period the capture rates were consistently low. Mean capture rates in the post-logging period were higher but also more variable. Although the data indicate that *C. signifera* is disturbance adapted, the high variability of capture rates meant that no silvicultural treatment was more favourable to the species than any other.

INTRODUCTION

Information on the response of amphibians to anthropogenic habitat alteration, especially that relating to the impacts of forest harvesting, is limited in Australia (Hazell 2003). Internationally, however, similar limitations are not apparent. Elsewhere, especially in North America, the responses of amphibians to logging have been shown to be highly species specific (deMaynadier and Hunter 1995). In their review of the literature, deMaynadier and Hunter (1995) identified microhabitat features as an important determinant of a species' presence or absence. Features such as coarse woody debris, litter depth, understorey vegetation, canopy closure, moisture, light levels, temperature, and pH have all been shown to influence the abundance of different amphibian species. It is possible that alternative silvicultural practices inadvertently retain some of these microhabitats, thus mitigating the impacts of traditional harvesting practices.

Seasonal environmental differences may also regulate the activity patterns of amphibians. Because they are ectothermic, anuran body temperatures are strongly related to ambient environmental temperatures. Amphibians also have moist, permeable skin and are susceptible to desiccation. Because of a trade-off between body temperature and water balance (Navas 1996), amphibian activity is often regulated by a combination of temperature and rainfall (Lemckert 2001). Bellis (1962), for example, found that the degree and duration of wood frog (*Rana sylvatica*) activity decreased with decreasing humidity. He also found that the average body size of frogs was greater in drier habitats, presumably because larger frogs have a smaller surface area to volume ratios and are, therefore, less prone to dehydration.

In this study I investigated seasonal activity and the effects of silvicultural practice on the frog *Crinia signifera,* with a view to shedding some light on the implications of microhabitat modification to this abundant ground-dwelling frog.

METHODOLOGY

Study Species

Crinia signifera is widely distributed throughout Tasmania and south-eastern mainland Australia. It is found in a wide range of habitats (Robinson 1996) and has a flexible life history. It breeds in both permanent and ephemeral sites and, in Tasmania, breeding is limited to lentic systems. Breeding in the Southern Forests of Tasmania occurs predominantly between early spring and mid summer and any autumn breeding seems dependent on rainfall (pers. obs.). The frog has an adult snout-vent length (SVL) of 20-30 mm and metamorphs have an average SVL of 9.1 ± 1.0 mm (pers. obs.). Metamorphosis occurs predominantly in January and February.

Study Area

The study area was located at the Warra Long Term Ecological Research (LTER) site. The Warra LTER is located within the Southern Forests of Tasmania, approximately 60 km south of Hobart (43°3'S; 146°39'E) and has an elevation range of 37-1260 m (Brown *et al.* 2001). The specific aims of the Warra LTER centre on developing an understanding of ecological processes in Tasmania's wet *Eucalyptus obliqua* forests and

the demonstration and development of sustainable forest management practices (www.warra.com).

Standard logging practices in wet and mixed sclerophyll forests consist of clearfell, burn and aerial sowing with eucalypt seed (CBS) on a rotation of 90 years (Hickey and Neyland 2000). Trials have also been established at the site to investigate alternative silvicultural practices. One investigative sub-component of these silvicultural trials is to measure the response of invertebrates to alternative silvicultural practices (see Bashford *et al.* 2001). The *Crinia signifera* specimens I used in my study were obtained as a result of by-catch from wet pitfall traps used in this invertebrate study.

To December 2002, pre-logging and the first phase of post-logging invertebrate sampling had been completed in five coupes. The silvicultural practices used in each coupe are presented in Table 24 and represent four different experimental treatments. The control treatment remained both unlogged and unburned throughout the study period. The dispersed retention silvicultural treatment maintained 10% of pre-harvesting eucalypt basal area but cleared both remaining over and understorey. The CBS ± understorey islands tested two types of harvesting treatments. Coupes were harvested using standard logging practices (CBS); however, understorey islands of dimensions 40 x 20 m were also retained. For further details regarding these silvicultural treatments see Hickey *et al.* (2001).

Table 24. Silvicultural Treatments in Coupes (from Bashford *et al.* 2001; Hickey *et al.* 2001)

Coupe	Silvicultural Treatment	Area of Coupe (ha)	Number of Sites	Burn Intensity	Seed Source
1B	10% dispersed retention	15.7	3	low	natural seed fall
8C	10% dispersed retention	11.1	2	low	natural seed fall
8B	CBS ± understorey islands	17.7	2*, 2#	high	sowing
8H	CBS ± understorey islands	26.0	4*, 4#	high	sowing
8J	control	35.0	3	none	none

* understorey island sites

CBS sites

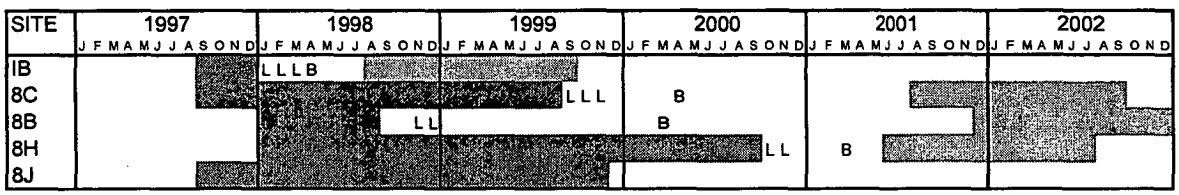
The number of sampling sites located within each coupe is presented in Table 24. Each site consisted of a 50 m transect having 10 pitfall traps. Pitfall traps were arranged in pairs each separated by 1-2 m. Pitfall traps consisted of 9 cm diameter, 15 cm long stormwater pipe set vertically into an augered hole in the soil. A 425 mL plastic cup charged with 100 mL of either 33% ethylene glycol (Castrol RadiCool®) or undiluted ethylene glycol (Castrol) was set inside each pipe. For further detail regarding pitfall trap construction refer to Bashford *et al.* (2001).

Figure 22 indicates the timing and duration of sampling in each coupe. Coupes were sampled for as long as logistically possible in the pre-logging phase. Pitfall traps were relocated at the same positions within each site after logging and burning. Post-logging sampling commenced as soon as feasible after burning and continued for a period of 12

months. Pitfall traps were continuously open during both the pre and post-logging periods and sampling was undertaken at monthly intervals.

Because sampling effort was unequal in different treatments, captures were converted to capture rates (captures per 1000 trap days) in order to enable comparisons to be made.

Figure 22. Timing and duration of sampling at coupes (L = logging, B = burning, dark bars = pre-logging sampling period, light bars = post-logging sample period).



Crinia signifera specimens were stored in 70% ethanol after field collection. Each specimen was patted dry with paper toweling before mass was measured using an electronic balance (± 0.005 mg) and SVL was measured using calipers (± 0.05 mm). Sex was determined bymorphological characteristics (males have grey and females have white colouring on the ventral surface of the chin). Because juveniles of either sex also have grey ventral chin colouring, smaller specimens were dissected to determine sex.

Statistical Analysis

To account for any bias in capture rates resulting from topography and the associated floristics, I categorized the location of all sites as either at the top, middle or bottom of the slope. I applied the Kruskal-Wallis test to investigate differences in capture rate.

ANOVA was used to determine any differences in SVL with season.

Because there was only one control site and sampling at this site did not overlap with post-logging sampling in other coupes I was unable to determine differences in capture frequency statistically; i.e. I was unable to separate effects due to logging treatment and the different time periods in which sampling took place. To compare capture rates in pre and post-logging sampling, I plotted the mean ± standard error of capture rates per 1000 trap days for each silvicultural treatment.

RESULTS

Kruskal-Wallis test showed that capture rates did not differ between the three topographical categories (upper, mid and lower slope) (Asymp. Sig = 0.299). As a result these data were pooled for subsequent analyses.

Fifty-two males and 71 females were captured. In addition there were 65 juveniles under the age of 1 (including 28 for which sex could not be determined).

Seasonal variations in capture rates are presented in Table 25. Capture data indicated that frogs were most active within the forest litter during summer and least active during winter. Capture rates in spring and autumn were intermediate. Juveniles were most abundant in the landscape in summer. Males were caught more frequently than females in autumn and females were apparently more active than males in winter. The activity rates of males and females did not differ in summer and spring.

Table 25. Seasonal variation in the total number of all frogs, juveniles, females and males (per 1000 trap days) and sex ratios

Season	All frogs	Juveniles	Females	Males	Sex ratio (f/m)
Summer	1.75	0.18	0.68	0.63	1.08
Autumn	0.79	0.02	0.22	0.37	0.60
Winter	0.21	0.01	0.13	0.08	1.50
Spring	0.94	0.02	0.37	0.31	1.17

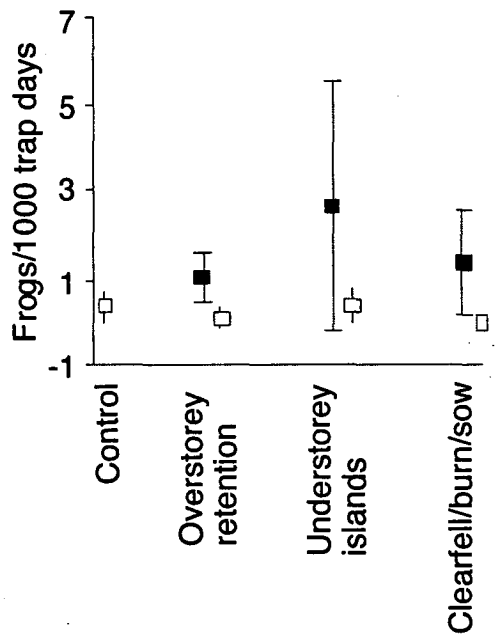
Seasonal variations in body size are presented in Table 26. Larger males were trapped in summer (SVL: mean ± SE: 22.4 ± 0.75 mm) than in autumn (19.4 ± 1.00 mm) and winter (18.4 ± 1.94 mm). Larger females were trapped in winter (SVL: mean ± SE: 30.6 ± 1.51 mm) than in summer (25.4 ± 0.62 mm) or autumn (25.4 ± 1.23 mm).

Table 26. Seasonal Variation in body size

Sex	*d.f.*	*F*	*P*
Males	3,59	2.931	0.041
Females	3,65	3.836	0.014

Mean capture rates in different silvicultural treatments are presented in Figure 23. Capture rates were consistently low in the pre-logging period. Mean capture rates in the post-logging period were higher but also more variable.

Figure 23. Mean (± sd) of total frogs captured per 1000 trap days in pre (open squares) and post (filled squares) logging periods for different silvicultural treatments



DISCUSSION

Despite the fact that *C. signifera* is common in disturbed habitats (pers. comm. F. Lemckert cited in Kavanagh and Webb 1998; Margules *et al.* 1995), higher capture rates in the post-logging period cannot be attributed unequivocally to logging treatment. This is because 1) there was only one control plot, 2) the control plot was not sampled concurrently with post-logging treatments and 3) sampling before and after logging was

almost mutually exclusive in time. It was, therefore, difficult to separate the effects of logging treatment from factors such as differences in climate during the pre and post-logging time periods.

Post-logging sampling in one coupe (1B), however, did overlap pre-logging sampling for the remaining coupes. Mean traps captures were much greater in coupe 1B (3.6 individuals per 1000 trap hours) during the post-logging period than the pre-logging period in the other coupes (mean of 0.22 individuals per 1000 trap hours), indicating that differences in pre and post-logging abundance of *C. signifera* are likely to relate to logging treatment and not temporal environmental differences.

Kavanagh and Webb (1998) also reported a low abundance of *C. signifera* in the unlogged forests of southern NSW and higher relative abundance both immediately and eight years after logging (although their study also suffers limitations relating to lack of replication - thus limiting statistical interpretation). Lemckert (1999), on the other hand, found that the abundance of *C. signifera* in the commercial forests of northern NSW decreased within increasing distance from a reserve and with increasing rainfall (a factor that may be related to increasing abundance of ponds in dryer forests: pers. comm. F. Lemckert) but not logging disturbance. Margules *et al.* (1995), found that the abundance of *C. signifera* decreased for four summers in eucalypt forest fragments after the surrounding area had been cleared to establish pine plantations but increased again after this time.

Higher abundance of *C. signifera* may reflect a higher abundance of standing water after logging. The construction of ponds as water supplies for the management of fire has undoubtedly increased the abundance C. *signifera* in the commercial forest landscape as a whole, but this does not necessarily explain why fewer individuals moved through unlogged than through harvested coupes (since these ponds are not constructed only adjacent to and within logged areas). The process of harvesting itself, however, may make the harvested habitat wetter through soil compaction (Wronski 1984) and reduced transpiration. As a result, it may be more hospitable to *C. signifera*. I found water puddling to be twice as common in logged coupes than in unlogged forest; however, it must be noted that the amount of this type of standing water *suitable for breeding* did not differ between logged and unlogged forest (my unpublished data), presumably because it was not judged as being large enough to sustain tadpole development before drying out.

No clear differences between silvicultural treatments were evident because treatments with higher mean abundance also had greater variability. Greater variability in the post-logging environment may reflect a concomitant increase in environmental variability. By reducing litter depth and canopy closure, for instance, moisture and temperature conditions are likely to be less buffered. My experimental findings do not indicate that any particular silvicultural practice consistently favours *C. signifera*.

Seasonal environmental variability did have consequences for activity patterns. Because *C. signifera* breeds predominantly in spring and early summer, movement during that time is expected to entail direct migratory travel to and from breeding sites. But because

breeding is metabolically costly, foraging after the breeding season is needed to replenish body condition, thus accounting for the high activity levels which occurred in summer. Males were more active than females in autumn suggesting that their foraging may be extended relative to that of females. This may be because males spend extended periods calling at the breeding site whilst females visit for only short periods. It is also possible that these data reflect differences in dispersal after the breeding season.

Higher abundance of juveniles in summer correlated with the peak period of metamorphosis. Larger males were more active in summer than in autumn and winter, presumably because they are less prone to desiccation than smaller males. Female biased sexual size dimorphism means that similar size limited movement is less likely for females. Although *C. signifera* do not hibernate during winter, they were less active during this time. Interestingly, females were more active than males in winter. These females were also larger than females trapped in autumn and summer.

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